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THE ECOLOGY OF CHIRONOMIDAE IN STORAGE RESERVOIRS.

By J. H. MUNDIE.

(*Imperial College, London**).

[Communicated by Mr. P. Freeman].

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With 1 Plate and 36 Text-figures.

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* Now at the Freshwater Biological Association, The Ferry House, Ambleside.

I. INTRODUCTION.

1. *The Place of Surveys in Chironomid Studies and the Objects of the Present Investigation.*

THE non-biting midges (Chironomidae = Tendipedidae), situated within a complex of the nematocerous Diptera, are best known as the predominant insects of lake sediments. In these the larvae may be present in great numbers and as detritus, animal, or plant feeders take part in the exchange of substances within the sediments and between them and the overlying water.

Apart from taxonomic studies, knowledge of lake chironomids has advanced along three main lines: those of zoogeography, physiology and productivity. The zoogeographical studies have been bound up with attempts to classify lakes, the various species of chironomids predominating in the profundals of different lakes being taken as indicators of different degrees of lake productivity. The physiological work on larvae has been largely concerned with feeding mechanisms and respiration, and has a close bearing on ecological problems. Productivity studies of chironomids are not yet far advanced. Numerous estimates have been made of standing crops of larvae in lakes, but it is only within recent years that attempts have been made to elucidate the causes of high or low productivity. These attempts have shown that an understanding of productivity demands, amongst other things, the analysis of complex food-chains, the working out of the life-cycles of individual species, and the measurement of metabolic rates.

Each of these three aspects of chironomid biology will be touched upon in a faunistic survey of a lake, but, as can be seen from Thienemann's (1954) extensive review of the literature on the distribution and ecology of chironomids, the point is now being reached where general short-term surveys of the chironomid faunas of lakes are likely to prove insufficiently intensive to add much new knowledge. This being so, any projected survey must be justified on the grounds of the thoroughness with which it answers the basic questions of the identity, locality and quantity of organisms in a selected environment. If this can be done satisfactorily in an environment which has permanence and is readily accessible, then the analysis of population interactions can be begun where the work of the survey leaves off.

The present investigation deals with the distribution and seasonal changes of the chironomid fauna of two storage reservoirs in Middlesex and includes observations on a third. Among the features which seemed to warrant the investigation at the outset was the simplification presented by a reservoir of some of the problems met with in lakes, *e.g.* the homogeneity and uniform slope of the littoral zone which suggested that sharp limits would be found to the distribution of the species living there. Other features in its favour were the intensiveness with which it was possible to carry out the investigation, and the opportunity it provided for applying new or little-tried techniques. Moreover, little was known about the midges of reservoirs as opposed to lakes, and in texts on the biology of water supply they received only a mention or were omitted.

The main questions which the survey set out to investigate were the qualitative and quantitative distribution of the chironomid species at each metre depth-zone, the bearing which this distribution has on what is known of the

biology of the species, the sequence of emergences of the different species throughout the year, the number of generations, and the annual production of chironomids at different depths. In the course of the work many other questions inevitably arose, of which those concerning the reliability of sampling methods were conspicuous.

2. Acknowledgments.

The period of this investigation was from February, 1950 until February, 1953, except for the analysis in 1954 of a series of samples kindly obtained for me by the Metropolitan Water Board. During the period August, 1950 to February, 1953 I was in receipt of a maintenance grant from the Nature Conservancy.

The work was carried out at Imperial College Field Station, Silwood Park, Sunninghill, Berks., then directed by Prof. J. W. Munro, C.B.E., for whose support I am much indebted.

My best thanks go to Dr. W. F. Jepson and to Dr. F. Greenshields for their support and advice throughout the investigation. The Metropolitan Water Board, on whose reservoirs the work was done, generously provided transport facilities and field equipment, including the traps used and the Jenkin surface mud sampler. Mr. J. Baker, Mr. A. Kemp and Mr. D. Lee, of the Metropolitan Water Board, took part in all the field work and without their skill and patience the survey could not have been carried out. I am further indebted to Mr. J. Baker for oxygen determinations.

I am indebted to the Metropolitan Water Board and to the Freshwater Biological Association for their sharing a grant towards the cost of publishing this paper.

I wish to express my gratitude also to Mr. P. Freeman for help with the taxonomy of chironomids, to Miss C. Kipling for help with statistical matters, to Mr. R. G. Davies, Dr. C. H. Mortimer and Mr. H. C. Gilson for advice and criticism, and to Mrs. F. J. Mackereth for identifying Trichoptera.

I am indebted to the Air Ministry, Meteorological Office, for wind tabulations.

3. The Reservoirs.

The reservoirs studied belong to the Metropolitan Water Board. They are Kempton Park East Reservoir (Nat. Grid Ref. 51/119708) (fig. 1), Staines South Reservoir and Queen Mary Reservoir. All lie in Middlesex and receive their water from the River Thames, Kempton Park Reservoir being supplied indirectly from the Queen Mary Reservoir. The following table gives approximate morphometric data :

TABLE I.—*Morphometric data.*

Reservoir.	Area (hectares).	Maximum depth (metres).	Capacity (cubic metres).
Kempton Park East Reservoir	16.18	7.0	909,000
Staines South Reservoir	99.55	9.0	7,980,000
Queen Mary Reservoir	292.59	10.5	30,700,000

The sides of the reservoirs have a slope of 1 in 3.

Queen Mary Reservoir is in constant use and its level is maintained, whenever

possible, by pumping water from the river. Staines South and Kempton Park Reservoirs, however, are standing reservoirs, *i.e.* they are used only at irregular intervals, chiefly during periods of drought, and have water supplied to them only after such periods. Both kinds of reservoir may be regarded as small lakes with highly uniform benthic zones. The reservoir in constant use may be considered as a lake with severely fluctuating water levels, and the standing reservoir as one in which replacement of water takes place at long intervals and where, therefore, a depletion of nutrients tends to occur after successive crops of algae.

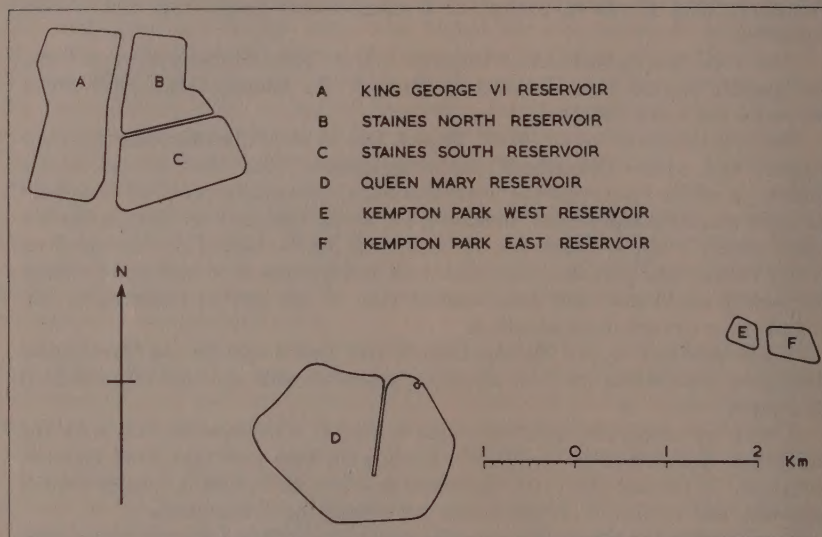


FIG. 1.—Sketch map of reservoirs studied, and adjacent reservoirs.

During the course of the survey Kempton Park East Reservoir was drawn upon rarely. In the second half of 1950 the maximum depth of water was 7.2 m., but when observations were resumed in March, 1951 it was 6.8 m. It remained at this depth throughout 1951. At Staines South Reservoir the maximum depth fluctuated between 8.8 and 9.1 m. Changes in water level at Queen Mary Reservoir were not recorded as observations of adult chironomids only were made there.

The generally used terms littoral, sublittoral and profundal can be applied without difficulty to reservoirs, although here, as in lakes, their limits vary with the seasons and cannot be strictly defined. The littoral zone extends from the water's edge to the limit of rooted vegetation. Since the sloping sides of the reservoirs are paved with concrete slabs which extend downwards, at least in Kempton Park East Reservoir, a distance of about 10 m. from top water level, and which are covered with only shallow deposits, rooted vegetation is restricted to *Chara* and small numbers of *Potamogeton*. The lower limit of the littoral is therefore probably about 4 m. The profundal—the region below the light-

controlled limit of rooted vegetation—is reached at a shallow depth, probably about 6 m. It is characterised by deep deposits and a deficiency of oxygen in midsummer. It is convenient to use the term sublittoral for the intermediate zone. In this region, which is beyond the limits of the concrete slabs, the substratum consists of gravel particles lying near the mud surface or completely exposed by water movement. These occur only occasionally in the littoral, and in the profundal are covered by at least 20 cm. of sediments.

II. METHODS.

1. *Biological Sampling Methods.*

(a) *The collection of chironomids for identification.*

The bulk of the data was derived from pupal or adult midges caught in submerged traps. Many of these were dead or wet and damaged on being removed from the traps, hence all were preserved in alcohol. It was impracticable, on account of the large number involved, to divide them into pinned and preserved specimens. Moreover, for the routine rapid examination of large numbers of chironomids under a stereoscopic microscope preserved material must be used, for hypopygial characters are then usually visible and the measurement of leg and antennal ratios is facilitated. Nevertheless initial identifications should be made, whenever possible, from pinned adults (Edwards, 1929).

To obtain dry and undamaged chironomids for checking the identity of the trapped material, collections of adults were made with a parachute-nylon net on the banks of the reservoirs at least once a week throughout summer and early autumn, and whenever adults were to be found in late autumn and spring. By this means pinned specimens were obtained of nearly all the trapped species. This procedure, however, did not assist in the separation of trapped female members of pairs of closely related species which were indistinguishable when their colours faded on preservation, e.g. females of *Procladius choreus* Meig., *P. crassinervis* Zett., *Cricotopus dizonias* Meig. and *C. bicinctus* Meig. This difficulty is inherent in the trapping method.

The net collections were also used to find if there were any conspicuous discrepancies between the commonest species taken on the wing and those most frequently trapped, to catch species not caught in traps, and to catch mating pairs so that the sexes could be associated.

Both pupae and pupal exuviae were found in the traps. The specific identities of these were established by rearing adults which were associated with their cast pupal skins. Larvae were obtained for rearing by means of a bottom dredge of the type illustrated by Welch (1948 : 310, fig. 82 right), but having a triangular frame at the rear as well as the leading end. The dredge was fitted with a brass gauze of 60 meshes per inch and protected on the outside by half-inch wire netting. It worked well from a boat over the profundal and was thrown from the shore to take samples from shallow water. All samples were washed on a 60-mesh gauze and the residue transferred to continuously aerated water in separate muslin-covered glass tanks. Numerous adults were reared in these and their pupal exuviae collected from the water surface.

(b) *Emergence traps.*

Emergence traps were used primarily to identify the insects in each metre depth-zone (adults are often identifiable whereas larvae are not); to make qualitative and quantitative comparisons of the faunas of different zones; to find the numbers and weights of insects produced per unit area of habitat in a given time; to study the sequence of emerging species throughout the seasons; and to determine the number of generations per year for each species.

The working principle of the submerged trap is that, if a funnel of metal gauze with a jar at its apex is lowered below the water surface, air is trapped in the jar and ascending pupae entering the funnel pass up into the jar and give rise to adults in the enclosed air space. The area of the mouth of the traps used was 0.25 sq. m.

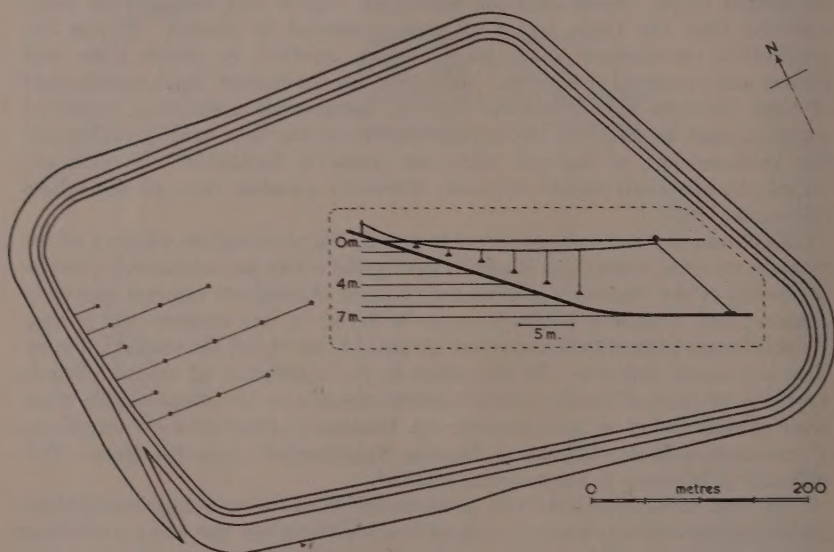


FIG. 2.—Plan of lines at Kempton Park East Reservoir.

Inset: side view of a 25-m. line.

The trap may be accepted as a quantitative sampling apparatus if insects do not avoid it; and the catch may be taken as having come from the area of substratum immediately below the trap if water movements do not introduce a horizontal component to the ascent of the pupae. These assumptions are certainly not always valid. They are discussed by Mundie (1956a), along with a description of the traps used on the reservoir and of the method of laying them out.

On Kempton Park East Reservoir 27 traps were used; on Staines South Reservoir 12, and they were set out along lines of lubricated pre-galvanized steel wire rope. Only one line was used on Staines South Reservoir and it ran from

the south-east corner. Its inshore end was secured underwater because of interference by the public. Consequently the first trap was set in 2 m. of water (fig. 4). At Kempton Park East Reservoir six lines were used (figs. 2 and 3). The traps at depths 1-6 m. were hung on 25-m. lines and not on the long lines, as wires used for sampling larvae (Mundie, 1956*b*) were attached to these over the 1-6 m. zone.

At Kempton Park East Reservoir the traps were emptied twice weekly from 21st September, 1950, to 27th October, 1950, and from 22nd March, 1951, to 25th October, 1951. Prior to this sampling was done once a week, but it

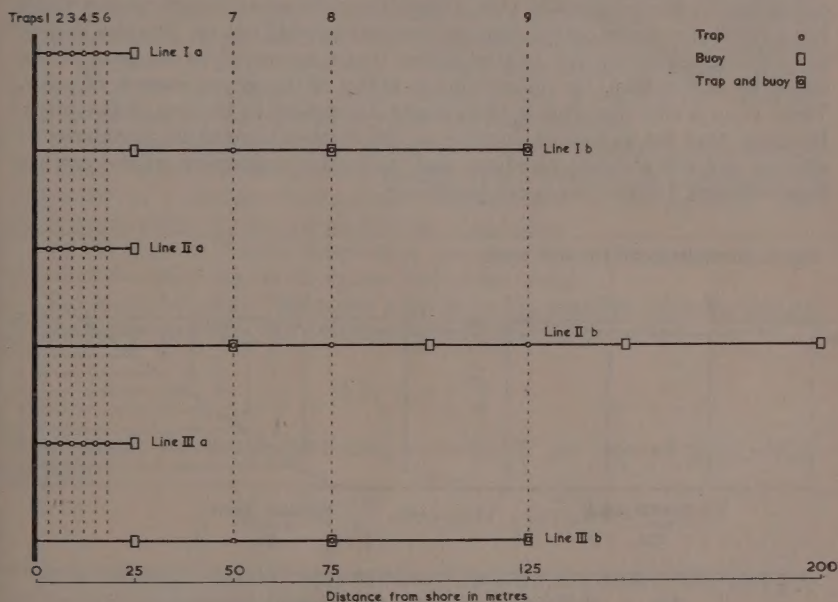


FIG. 3.—Plan of lines and traps at Kempton Park East Reservoir.

was found that part of the catch disintegrated in this time because of fungal attack. At Staines South Reservoir the traps were examined at weekly intervals from November, 1950 until March, 1951 to find if there were any emergences in winter (none was recorded), and then twice weekly on the same dates as the Kempton Park East Reservoir traps were examined.

A metal boat fitted with an outboard motor was used throughout the work. The sampling procedure and sources of faulty sampling are described by Mundie (1956*a*).

The traps were set about 1 m. above the substratum in order to minimise the intrinsic sources of error. These are: the avoidance by the insects of the traps because of their opacity, the possible effects of horizontal water movements on the pupae, and the predation of the pupae by fish (mainly perch). Each of these factors will vary with the depth-zone and, consequently, together

they make direct quantitative comparison of littoral and profundal catches unjustifiable.

Yet another source of error is the activity of animals other than chironomids within the jar of the trap. In Staines South Reservoir catches often included dozens of water mites of several species. It is quite likely that these prey on the midges. Minnows do not seem to enter traps. Only small ones (8 mm. long) were caught and these would not be feeding on chironomids.

A reliable estimate of the efficiency of the traps, therefore, cannot be reached in the ordinary course of field-work, but could only be made under experimental conditions. In the field one can relate catches to changing numbers of larvae and pupae on the bottom and this is best done with an abundant species which has a short emergence period, but, as has been pointed out by Mundie (1956a), the difference between the two estimates is not necessarily a measure of the efficiency of the trap, for no account is taken of the above sources of error. There is no doubt that this is the greatest limitation to the use of the traps. It means that for any given depth-zone the catches have to be considered as relative and not absolute numbers, and that strict comparison of the catches from different depth-zones is not justifiable.

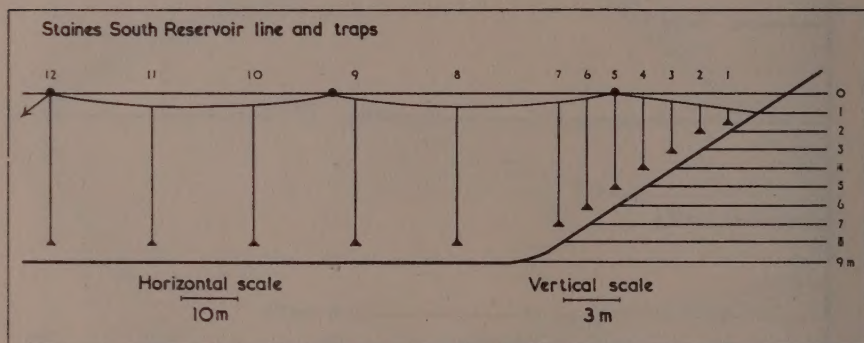


FIG. 4.—Side view of the line at Staines South Reservoir.

Trapping efficiency is further discussed in the section on the relation between trap and core estimates (p. 209).

The sites for the lines on the reservoirs were selected largely as a matter of convenience, the attachment points on the shore being made near places where the boat could easily be unloaded from the trailer and launched. As a result, the lines at Kempton Park East Reservoir traversed an area of water sheltered from the prevailing westerly wind by the reservoir bank, whilst at Staines South Reservoir the line, running from the south-east corner, lay in a region where wave action was particularly strong. The catches from here are, therefore, not considered to be representative of Staines South Reservoir as a whole. They tended to be erratic and low, owing, it seems, to the effects of waves on the ascending pupae, and to the scantiness of the deposits which form a substratum for the larvae. The emptying of traps, moreover, was particularly difficult here on windy days, and it is possible that catches were occasionally lost.

(c) *The sampling of larvae.*

The objects of sampling larvae in the profundal of Kempton Park East Reservoir were to estimate the population at 6.8 m. throughout the year, to find if there was any variation in numbers at different distances from the shore (all at 6.8 m. depth) and to correlate changes in the larval population with the trapping results. The sampler used was a Jenkin surface mud sampler, mounted on a davit (Plate I). This instrument is described by Mortimer (1942). It lifts an undisturbed core of mud within a perspex tube of internal cross sectional area 36.29 sq. cm.

Some remarks may be made on the subject of estimating benthic populations, as this is usually given scant treatment by limnologists. It is clear that the greater the number of larvae taken to estimate the mean of a population the more accurate will be the estimate. A single large sample, however, gives no measure of the variability of the population within a depth-zone. This can only be assessed by taking a large number of small samples.

To find the number of small samples (*i.e.* cores) required to estimate the population with a given degree of accuracy it is convenient to argue from the properties of a random distribution. Measurement of the departure from randomness shown by the population can then follow.

In a random or Poisson distribution the mean equals the variance and the standard deviation equals the square root of the mean.

The standard error of the mean is given by the standard deviation divided by the square root of n , the number of sample units or cores, *i.e.*

$$\text{S.E. } \bar{m} = \frac{\sqrt{\bar{m}}}{\sqrt{n}}$$

Since sample means are distributed normally, 95 per cent. of them will lie between

$$\bar{m} \pm 1.96 \frac{\sqrt{\bar{m}}}{\sqrt{n}} \text{ or roughly } \pm 2 \frac{\sqrt{\bar{m}}}{\sqrt{n}}$$

It is necessary to select a level of accuracy for the count. The accuracy is here expressed as the count $\bar{m} \pm y$ per cent. of itself.

Then

$$\bar{m} \times \frac{y}{100} = 2 \frac{\sqrt{\bar{m}}}{\sqrt{n}} \text{ i.e. } n = \frac{40,000}{y^2 \bar{m}}$$

If a 10 per cent. accuracy is chosen, then $y = 10$ and $n = \frac{400}{\bar{m}}$.

In a Poisson distribution the count from a single core can be taken as the mean. Therefore, if a core count is 40, the number of cores necessary to sample the population with 10 per cent. accuracy is 10. Similarly, if the count is 100, n is 4, and if the count is 400, n is 1. It is therefore clear that to achieve a desired accuracy of 10 per cent., the total number of larvae counted from a Poisson distribution should be 400 and it is immaterial whether this is done from one sample of benthic material or many small ones.

In all likelihood a benthic population will be found to deviate from random-

ness, and to occur in patches. The nature of the patches revealed will depend on the size of the instrument used for sampling.

In the reservoir survey it was not known how great the departures from randomness would be throughout the seasons, nor how detailed an analysis would be possible of the individual species found in the cores. Furthermore, cores had to be preserved to await analysis, it being impossible to deal with them as they were collected. A somewhat arbitrary number, therefore, of 12 samples, each of two cores lumped together, was taken for the routine monthly sampling procedure, although initial counts showed that this was more than was required to estimate the means of the population as whole. In the course of time this decision was seen to have erred on the side of taking too many cores too infrequently. It would have been more informative to have taken 12 single cores once a fortnight.

Figure 34 (p. 212) gives the number of samples taken from Kempton Park East Reservoir and the results of the analysis. Adjustments have been made to plot all the data on one scale. These are stated in the legend.

For assessing deviations from randomness shown by low counts (less than 50), comparison can be made of the counts with a table of confidence limits for the Poisson distribution. For higher numbers, Fisher's coefficient of dispersion (Blackman, 1942) may be used. Its application to animal distributions is exemplified by Salt and Hollick (1946) for wireworm populations. The reservoir samples show high aggregation in summer (*e.g.* coefficient of 10 in June and September, 1951; randomness shows a coefficient of unity) but may show much more even distribution in late winter or spring (*e.g.* coefficient of 0.8 in April, 1954).

In 1951, from May onwards, the samples were taken along the lines Ib, IIb and IIIb at 6.8 m. (fig. 3), four samples, each of two cores, being taken at each line and labelled 1-4, the first being nearest the shore, the fourth nearest the end buoy. It was subsequently found that single cores proved adequate for the purpose for which they were required and after March, 1952 these were taken. The samples in 1954 were taken along the sites of the lines.

At Staines South Reservoir only one series of 12 single cores lumped together was taken. This was done in the region of traps 7-12 on 10th May, 1951.

When a core was taken up from the bottom it was placed in a circular sieve about 30 cm. in diameter and 15 cm. high, with a copper gauze of mesh 0.25 mm. (*i.e.* 60 meshes per linear inch) and washed over the side of the boat. This procedure, more than any other, determined the degree of accuracy of the sampling. Limnologists working on bottom fauna generally use a 0.6 mm. gauze but this retains only the larger animals (Jónasson, 1955). Some first instar chironomid larvae pass through a 0.25 mm. screen so that a 100 per cent. removal of larvae cannot be claimed for the method. An 80-mesh gauze, however, proved impracticable in the field, for little of the mud would pass through it in the washing process.

About nine-tenths of the mud passed through the gauze so that a core of 360 m.l. would give a residue of about 30 m.l. This was transferred to a labelled wide-mouthed jar and taken to the laboratory where 80 per cent. alcohol was added. All cores had to be preserved in this way to await analysis.

One of the greatest obstacles to investigating the quantitative aspects of bottom fauna is the labour involved in removing, identifying and counting

the animals present in bottom samples, and any technique which might reduce the time required for these operations deserves close consideration. Particular difficulties are presented by chironomids in their great range of size (less than 1 mm.-2 cm.), their tube-dwelling habit (which limits the use of a flotation technique) and their close association with dense plant material in the littoral, or with filamentous bacteria (*Beggiatoa*) and dead organic matter in the profundal.

The following procedure was worked out for dealing with core samples :

(1) Pour the stored preserved sample into a circular 40-mesh sieve in an enamel basin ; add 70 per cent. alcohol and by agitating the sieve for several minutes wash as much as possible of the material through it.

(2) Transfer the 40-mesh residue (the portion left in the sieve) to a 500-ml. conical flask half-full of water. Add benzene to form a layer about 5-mm. thick on the surface, cork and shake very vigorously. Pour the mixture immediately into a 400-ml. beaker. Allow to settle, then transfer the floating portion (mainly plant material and chironomid larvae) to a small 90-mesh sieve. Pour industrial spirit through this to remove the benzene. Transfer the material to 70 per cent. alcohol and sort it, a little at a time, under a $\times 15$ stereoscopic microscope. Sort in a 5 cm. diameter petri dish marked off in squares using a black background.

(3) Transfer the material which had sunk in the beaker to 70 per cent. alcohol and examine in the same way.

(4) Take the 40-mesh sieve filtrate and screen as much as possible of it, in alcohol, through a 60-mesh sieve.

(5) Transfer the 60-mesh residue to water in a separating funnel (10 cm. diameter). Add benzene and a few drops of detergent, put on the stopper and shake very vigorously. Allow to settle. Run off the sunk portion into a small beaker, pour out the floating portion and wash with industrial spirit. Examine a little at a time as above, using a $\times 15$ magnification.

(6) Examine the sunk portion in alcohol.

(7) Repeat (5) and (6) with the 60-mesh filtrate.

The use of benzene to separate larvae from inorganic and some organic material is derived from Salt and Hollick (1944). Detergent is used to facilitate the sedimentation of sand.

As an example of the use of this method the double core sample I 3 lifted on 19th November, 1951 and analysed in May, 1952 may be taken.

	Minutes.
Sieving ; and benzene treatment of 40-mesh residue	30
Examination of floating portion (135 larvae)	30
Examination of sunk portion (44 larvae)	25
Sieving and benzene treatment of 40-mesh filtrate	10
Examination of floating portion of 60-mesh residue (23 larvae)	20
Examination of sunk portion (1 larva)	10
Benzene treatment of 60-mesh filtrate	5
Examination of floating portion (2 larvae)	20
Examination of sunk portion (0 larvae)	10

Total time : 2 hours 40 minutes.

Most double cores were done in less time than this. Clearly the last four operations could be omitted. The time required depends largely on the amount of fibrous material present, as the larvae have to be teased out of this.

The Jenkin surface mud sampler may be assumed to give a wholly valid sample, for the difficulties of jaws not closing fully and of sample "spill-over" which grabs present do not arise, and should it fail to shut properly on coming to rest then the sample, when lifted to the surface, is at once seen to be faulty. The only way in which it might fail to take all the animals below its area would be by not penetrating sufficiently far into the mud. At Kempton Park East Reservoir cores were rarely more than 15-cm. high and this is a shallow depth. In eutrophic lakes cores twice this depth are commonly obtained.

It was of importance, therefore, to ascertain the vertical distribution of the larvae within the mud. For this purpose four cores were taken on 17th March, 1952, and each was divided into bottom, middle and top thirds. To do this the water in the tube was siphoned out and a rubber bung placed in the upper end of the tube; the lower lid was then lowered and the mud allowed to fall out slowly.

TABLE II.—*Analysis of core samples from Kempton Park East Reservoir, 17th March, 1952. Depth of cores 14.0–14.5 cm.*

Sample.	Level.	Chironomid larvae.	Chironomid pupae.	Site of sample.
I	Top third	120	5	Line I
	Middle	2	0	1st Buoy
	Bottom	1	0	.
II	Top third	188	8	Line II
	Middle	9	0	1st Buoy
	Bottom	1	0	.
III	Top third	171	2	Line III
	Middle	3	0	1st Buoy
	Bottom	11	0	.
IV	Top third	159	4	Line IV
	Middle	4	1	1st Buoy
	Bottom	5	0	.

As can be seen from Table II, 95 per cent. of the fauna is in the top third and 2.5 per cent. in the bottom.

The average depth of cores taken beyond the first buoys of the three lines (50 m. from shore) was 10.0 cm. Cores taken nearer the shore, however, were invariably deeper, being about 14.0 cm. Attempts were made to obtain cores deeper than this by using the sampler without its legs and by adding lead weights to it. These attempts failed, however, for the cores obtained were in fact, no deeper.

In April another series of cores was taken for analysis of the vertical distribution of the larvae. The results obtained are shown in Table III.

TABLE III.—*Analysis of core samples from Kempton Park East Reservoir, 21st April, 1952.*

Sample.	Level.	Chironomid larvae.	Sample.	Level.	Chironomid larvae.
I .	Top 10 cm.	97	VII .	Top 5 cm.	171
	Bottom 2.0 cm.	1		Middle 5 cm.	2
II .	Top 10 cm.	137		Bottom 4.5 cm.	2
	Bottom 2.0 cm.	1	VIII .	Top 5 cm.	130
III .	Top 5 cm.	138		Middle 5 cm.	6
	Middle 5 cm.	2		Bottom 2.5 cm.	0
	Bottom 3.0 cm.	3	IX .	Top 5 cm.	134
IV .	Top 5 cm.	175		Middle 5 cm.	3
	Middle 5 cm.	4		Bottom 6.0 cm.	0
	Bottom 4.5 cm.	0	X .	Top 5 cm.	199
V .	Top 5 cm.	132		Middle 5 cm.	5
	Middle 5 cm.	6		Bottom 4.5 cm.	2
	Bottom 5 cm.	2	XI .	Top 5 cm.	171
VI .	Top 5 cm.	159		Middle 5 cm.	2
	Middle 5 cm.	4		Bottom 4.0 cm.	1
	Bottom 5 cm.	1	XII .	Top 5 cm.	189
				Middle 5 cm.	2
				Bottom 2.5 cm.	2

From these data it is seen that the fauna below 10 cm. is less than 1 per cent. of that in the top 5 cm. It was, therefore, assumed that no significant portion of the fauna was missed by using 10-cm. cores and, consequently, that the samples were valid.

The Jenkin sampler can only be used on deep sediments and could not therefore be used for sampling larvae on the littoral and sublittoral. A plate sampler was devised for doing this and is described by Mundie (1956b).

2. *Physical and chemical methods.*

Since the distribution of chironomid larvae in different habitats is bound up with their oxygen requirements, it was of interest to know the oxygen content of the sediments in the littoral and the profundal throughout the year.

The accurate analysis of the oxygen content of wet soils is a laboratory operation and could best be carried out on an undisturbed Jenkin surface sample. It was not practicable, however, to do this on the reservoir sediments and, moreover, the Jenkin sampler could not be used on the littoral. Samples of water collected close to the mud surface were therefore used to give a rough estimation of the oxygen at the surface.

To obtain a water sample the apparatus shown in figure 5 was made. It consists of a 350-ml. sampling bottle mounted on a rack made of discs of aluminium and brass rods. The bottle is filled over the edge of the boat with surface water. It is then placed on the rack (the disc which surrounds it slides down to allow its entry) and the bung is inserted. Through this pass two tubes, one of glass leading down to near the bottom of the bottle and having attached to its other end 10 m. of thick-walled pressure tubing, the other a short thin-walled, wide diameter rubber tube about 40-cm. long which passes from the bung to a central hole in the lowermost disc of the rack. The sampler is lowered to the bottom on a flexible stainless steel wire, which is attached to the pressure

tubing along its length. It comes to rest on three plates at the end of long legs which are so adjusted that the base of the rack is 2-3 cm. above the mud. An evacuated milk bottle is attached, in the boat, to the pressure tubing and when the vacuum is released by unscrewing a clamp the negative pressure draws

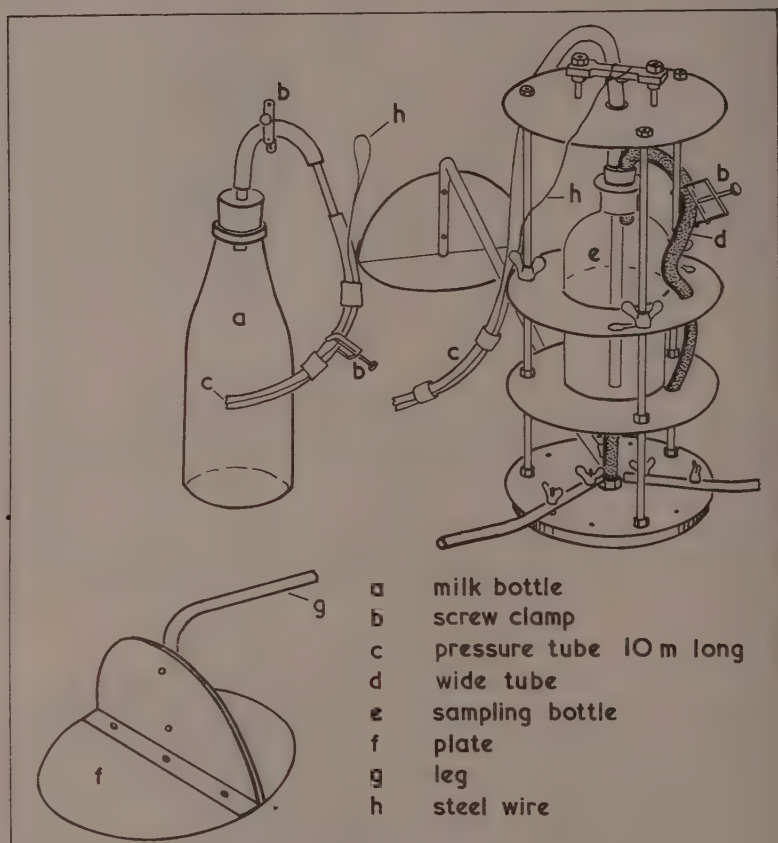


FIG. 5.—Water sampler for oxygen determinations.
(For explanation see text).

the surface water out of the sampling bottle up into the milk bottle. The surface water is replaced in the sampler by bottom water entering through the hole in the base of the rack and passing up the short wide tube into the sampling bottle. The hole is protected by a 40-mesh gauze which covers the base. Altogether four milk bottles are used to ensure a several-fold replacement of the water in the sampler. After the fourth has been filled (to within a few ml. of the top) the pressure tube is clamped, the sampler is pulled to the surface, the wide-necked tube is also clamped to prevent water being drawn up it from the bottle, and the bottle is removed. The temperature of the water is then taken and

manganous sulphate, alkaline iodide solution and sulphuric acid are added, as in the Winkler method of analysis (Welch, 1948: 208). The titration was done on return to shore.

The milk bottles were evacuated in the laboratory by means of a motor-driven vacuum pump.

As a rule five oxygen determinations were made at Kempton Park East Reservoir each week from March to October. The samples were taken at mud level below 1, 3, 5 and 6.8 m. of water (two samples at 6.8 m.). Several samples had to be discarded due to the presence of mud, which showed itself by the low estimate, if not visibly.

The method is open to criticism. It attempts to overcome the difficulties of obtaining a sample in the immediate vicinity of the larvae, and of having it free from particulate organic matter, by taking one from near the mud surface. This, however, is the region where the oxygen gradient, in summer, may be steepest. On the other hand, the larvae, by their respiratory movements, certainly draw upon oxygen from water above, rather than within the mud, but to what extent they do so is not known. Apart, therefore, from the fact that the estimates obtained (fig. 35) can be regarded as only indicative of the oxygen conditions, their significance in relation to larval respiration is by no means certain. Nevertheless they clearly show that the strong and lasting anaerobic conditions which may arise in the profundal of eutrophic lakes in mid and late summer did not develop in Kempton Park East Reservoir in 1951.

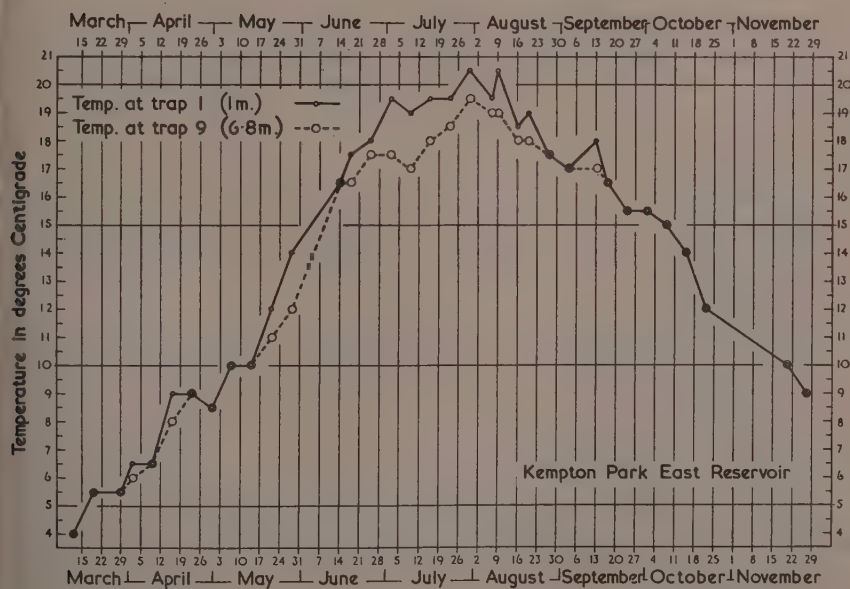


FIG. 6.—Water temperature near the mud surface at 1 m. and 6.8 m. in Kempton Park East Reservoir during 1951.

Furthermore, they show roughly the differences between the summer oxygen content of the littoral and profundal deposits. The establishment of these facts seems to justify the use of the sampler.

Organic carbon was determined by Walkley and Black's rapid titration method (Piper, 1944). The results are not affected by carbonates, but are affected by the presence of ferrous iron, *i.e.* ferrous sulphide (Southward, 1952), which gives too high an estimate for carbon. Ferrous iron is certainly present in the sediments but probably not near the mud surface, for under the aerobic conditions of Kempton Park East Reservoir it would be oxidised to ferric iron.

Accurate temperature measurements were not taken. Measurements were made to the nearest half degree, usually weekly, on water samples obtained from different depths by a Friedinger bottle. Readings are plotted on figure 6.

III. THE OCCURRENCE OF SPECIES IN THE RESERVOIRS.

Table IV lists the species dealt with, the nomenclature following, for the most part, that of Goetghebuer (1936-50) and Lenz (1936) in Lindner, *Die Fliegen der Palaearktischen Region*. It also indicates whether they were trapped or caught in swarms. In view of the limited number of observations made on Queen Mary Reservoir, the list for this reservoir can be taken as only preliminary. It is almost certain that all the species found in the other reservoirs could be found here also, at least in small numbers.

TABLE IV.—Occurrence of Chironomidae in three reservoirs.

T = trapped, *S* = caught in swarms only.

Species.	Kempton Park East Reservoir.	Staines South Reservoir.	Queen Mary Reservoir.
<i>Pentaneura carnea</i> Fabr.	S	.	.
<i>P. falcigera</i> Kieff.	.	.	S
<i>P. monilis</i> L.	T	T	S
<i>P. ornata</i> Meig.	S	.	.
<i>P. phatta</i> Egger.	S	.	.
<i>Anatopynia notata</i> Meig.	T	.	.
<i>Procladius crassinervis</i> Zett.	T	T	.
<i>P. choreus</i> Meig.	T	T	S
<i>Psilotanytus lugens</i> Kieff.	.	T	.
<i>P. rufovitatus</i> v.d. Wulp	T	T	S
<i>Orthocladus flexuellus</i> Edw.	S	.	.
<i>O. glabripennis</i> Goetgh.	S	.	S
<i>Chaetocladus perennis</i> Meig.	S	.	.
<i>C. piger</i> Goetgh.	S	.	.
<i>Dactylocladius semivirens</i> Kieff.	S	.	S
<i>Diplocladius cultriger</i> Kieff.	S	.	.
<i>Psectrocladius barbimanus</i> Edw.	T	.	.
<i>P. limbatellus</i> Holmgr.	T	T	S
<i>P. stratiotis</i> Kieff.	T	T	.
<i>Cricotopus bicornis</i> Meig.	S	.	.
<i>C. dizonias</i> Meig.	T	T	S
<i>C. sylvestris</i> Fabr.	T	T	S
<i>C. triannulatus</i> Mcq.	S	.	.
<i>C. trifascia</i> Edw.	S	.	.

Species.	Kempton Park East Reservoir.	Staines South Reservoir.	Queen Mary Reservoir.
<i>Nanocladius bicolor</i> Zett.	T	.	.
<i>Limnophyes</i> incert.	T	.	.
<i>Smittia atterrима</i> Meig.	S	.	.
<i>S. contingens</i> Walk.	.	.	S
<i>S. pratorum</i> Goetgh.	S	.	.
<i>Thienemanniella majuscula</i> (?) Edw.	S	.	.
<i>Diamesa guedii</i> Meig.	S	.	.
<i>Pseudochironomus prasinatus</i> Staeg.	T	.	S
<i>Chironomus anthracinus</i> Zett.	.	T	S
<i>C. cingulatus</i> Meig.	T	.	.
<i>C. plumosus</i> L.	T	T	S
<i>C. riparius</i> Meig.	S	.	.
<i>Limnochironomus lobiger</i> Kieff.	T	.	.
<i>L. nervosus</i> Staeg.	T	T	.
<i>L. pulsus</i> Walk.	T	T	S
<i>Cryptochironomus albofasciatus</i> Staeg.	T	T	.
<i>C. biannulatus</i> Staeg.	T	.	.
<i>C. psittacinus</i> Meig.	S	.	.
<i>C. redekei</i> Krus.	T	.	.
<i>C. suppicans</i> Meig.	S	T	.
<i>C. vulneratus</i> Zett.	T	.	.
<i>Parachironomus vitiosus</i> Goetgh.	T	T	.
<i>P. bacilliger</i> Kieff.	T	T	.
<i>Harnischia</i> sp.	T	.	.
<i>H. tener</i> Kieff.	T	.	.
<i>H. viridulus</i> Fabr.	T	T	.
<i>Glyptotendipes paripes</i> Edw.	T	T	.
<i>Endochironomus albipennis</i> Meig.	T	T	S
<i>Microtendipes chloris</i> Meig.	T	T	S
<i>M. pedellus</i> De G.	T	.	S
<i>Polypedilum nubeculosum</i> Meig.	T	T	S
<i>Micropsectra praecox</i> Meig.	S	.	S
<i>Tanytarsus lugens</i> Kieff.	T	T	S
<i>T. holochlorus</i> Edw.	T	T	S
<i>T. lestaei</i> Goetgh.	T	.	S
<i>T. verralli</i> Goetgh.	T	.	.
<i>T. sylvaticus</i> v. d. Wulp.	T	T	.
<i>Cladotanytarsus atridorsum</i> Kieff.	T	T	S

Total : 62 species.

IV. THE SPATIAL AND TEMPORAL DISTRIBUTION OF THE SPECIES WITH NOTES ON THEIR BIOLOGY.

1. Preliminary Remarks.

The use of the emergence traps established the identity, the zonation, the phenology and the voltinism of the species found.

In the following treatment taxonomic matter has been almost entirely omitted. The reader is referred to Hennig (1950) as a source of what is known of the morphology of immature chironomids. It has been necessary, however, to deal at length with the problem of the *Procladius choreus* complex, both on morphological grounds and in the light of the emergence data.

The general zonation of the species in Kempton Park East Reservoir is

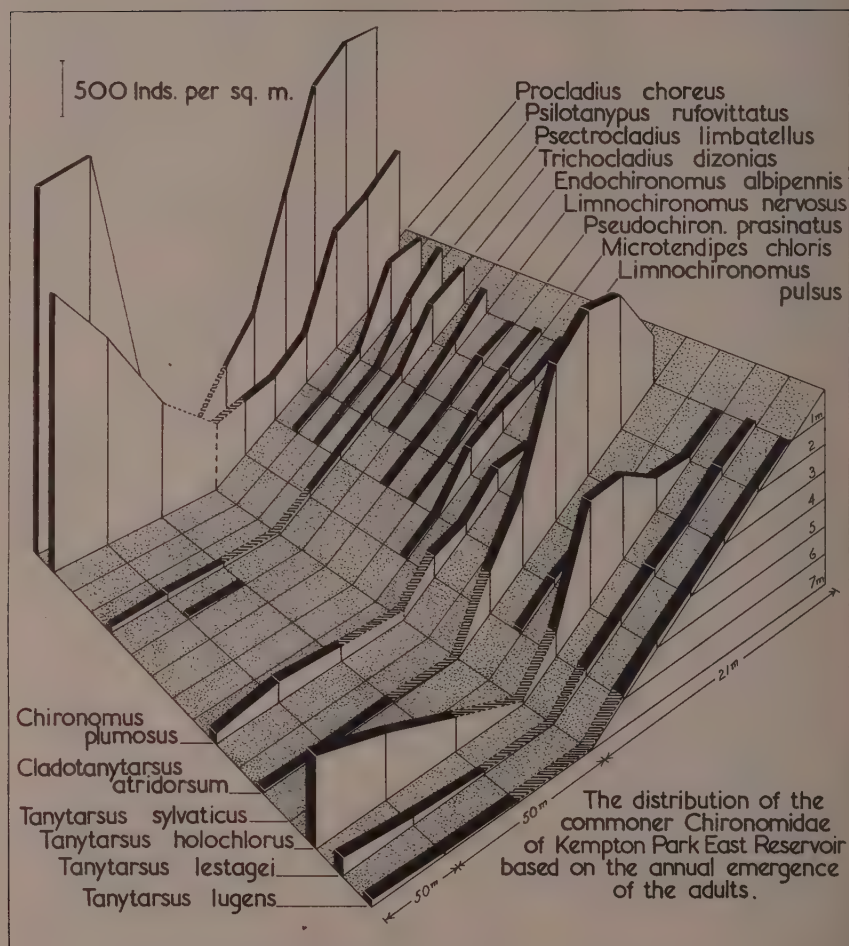


FIG. 7.—For explanation see text. (Fig. from Mundie, 1955).

summarised graphically in figure 7. In the zone 6–6.8 m. no trapping was done, so that the numbers indicated by hatching are conjectural. As is well known, the causes of zonation in animal distributions are complex and only intensive studies on the biology of the individual species will reveal what factors are most important. In the distribution of chironomids the nature of the food and the amount of oxygen in the habitat are clearly of significance.

As might be expected from a fairly large family (c. 3000 known species), the Chironomidae show a diversity of feeding habits. These have been studied by Leathers (1922) and Walshe (1951b) amongst others, and reviewed by Thiennemann (1954). Examples of some of these are given later.

The respiration of chironomid larvae is bound up in many genera with the utilisation of haemoglobin. The larvae are apneustic and the blood therefore functions in transporting oxygen. Much work has been done on the role of haemoglobin in respiration but a clear and full understanding of its function, particularly in relation to anaerobiosis, has not been reached. The subject has been very briefly reviewed by Buck (1953). It is sufficient for present purposes to point out that the Orthocladiinae (without haemoglobin), *Tanytarsus*, *Stictochironomus*, *Sergentia*, *Endochironomus* and *Chironomus* sen. str. are commonly regarded as a series with decreasing sensitivity to oxygen deficiency, both on the basis of their distribution in the profundals of different lakes and (for some genera) on experimental evidence (see references in Buck, 1953; and Brundin, 1951). The relationship between the distribution of the species in the reservoirs and their oxygen requirements is discussed below.

The phenological data derivable from the catches and presented along with the treatment of zonation are: the dates of the first and last emergences of a generation, the mean date of emergence, the mode, the standard deviation and the shape of the emergence curve. Some of the statistical issues connected with phenological observations of this kind are pointed out by Williams (1953), who stresses that errors tend to be in one direction, *i.e.* late.

The catches are expressed as histograms, the heights of the lines being equal to the total number of insects caught in three traps at a particular depth, that is, therefore, from three-fourths of a sq. m. Since catches were removed twice a week, however, the sampling periods were alternately three and four days. Adjustments to the counts have not been made for these, but the distances between the columns are proportional to the sampling periods.

Ideally examination of the histograms for all depths should show, for each species, its range and optimum depth in the reservoir, the number of generations it has in the year at different depths, the times of emergence, the shape of the curve (*i.e.* its skewness and kurtosis) and the effect of increase in depth on emergence time. The most concise presentation of a distribution is a statement of the mean and standard deviation. For the catches the latter can be most rapidly calculated, and with sufficient accuracy, by expressing the cumulative counts (frequencies) as percentages of the total frequencies and plotting them against the number of sampling occasions (1, 2, 3, . . .) on arithmetic probability paper. If the distribution of emerging insects is normal a straight line will be obtained; if it is positively skewed the points will lie on a curve which is convex to the abscissa. The method of deriving the standard deviation is given by Harding (1949) in a discussion of the graphical analysis of polymodal distributions.

It should be stressed that the histograms are to be regarded as based on relative numbers of insects, or at least on numbers which cannot be assumed to be absolute, and that the catches from different depth-zones are not directly comparable because of differences in trapping efficiency at different depths.

In a species with more than one generation per year the duration of the life-cycle is given approximately by the times between peak catches in successive generations. A source of error is the unknown delay between the emergence of the female and oviposition. Similarly, in a univoltine species the duration of a cycle is given by the time between the emergence in one year and that of the following. This period will be a function of the benthic temperatures.

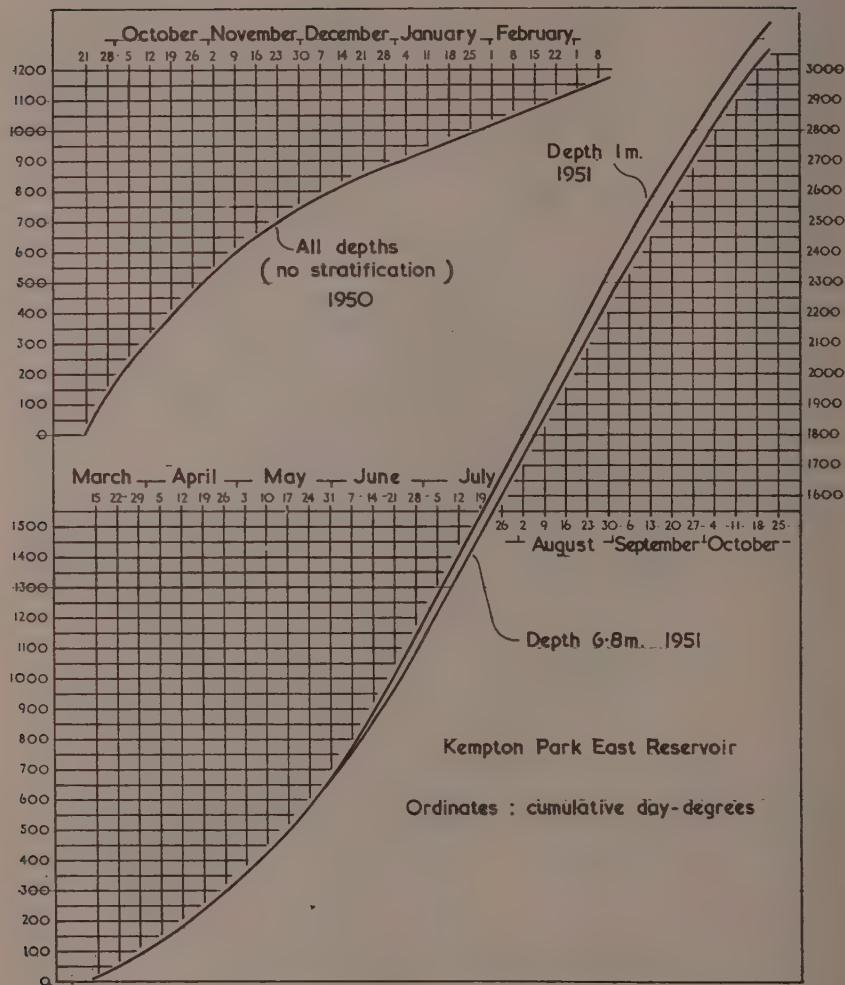


FIG. 8.—Cumulative day degrees near the mud surface at 1 m. and 6.8 m. in Kempton Park East Reservoir.

The relationship between the rate of development of an insect and the temperature at which development takes place is often described by the empirical formula

$$d(T - y) = K$$

where d is the time in days, T is the temperature, y is the temperature at which development ceases (the developmental zero) and K is a constant. The objections

to the use of this formula are numerous (see Wigglesworth, 1953 : 450). Nevertheless the thermal stability of a lake makes it usable and it is of interest to compare by means of it the day-degree requirements of different species. Although such information has only a descriptive value it is needed from different lakes and could easily be obtained.

In figure 6 the bottom temperatures at 1 m. and 6.8 m. are plotted from March to November and figure 8 shows the cumulative day-degrees up to October, 1951 and those of October, 1950 to the end of February, 1951. From this graph the day-degrees which have accumulated between any two dates may be read.

Since K in the formula is a constant

$$(T - y) d = (T_1 - y) d_1 = (T_2 - y) d_2 \dots$$

hence

$$y = \frac{T_1 d_1 - Td}{d_1 - d}$$

The use of this in calculating the temperature at which a species ceases development is illustrated below.

The difficulty of presenting ecological data lies in the fact that, whereas the many aspects of an animal's ecology occur simultaneously, their analysis must be presented in a sequence. Two methods of presentation are possible. One is the selection of subjects which are discussed separately, e.g. phenology, or the distribution of larvae in relation to some environmental factor; the other is the treatment, in turn, of all the findings appertaining to each species. The second method is the one adopted here as it is considered the most appropriate for a general survey. It allows the inclusion of miscellaneous information which would otherwise be difficult to place, but it has the disadvantage of tending to obscure, in the accumulation of detail, aspects of the fauna as a whole.

No sampling was carried out to find the time of day at which the chironomids entered the traps. The catches give no information on this, as they were all removed from the traps between 10.00 hours and 15.00 hours. Miller (1941) found that species which lived on the bottom above the thermocline emerged mainly between 04.00 and 07.00 hours, whilst those living below the thermocline emerged at any time of the day or night. Scott and Opdyke (1941) working on Winona lake found a maximum emergence from 18.00 to 24.00 hours, with a smaller peak between 04.00 and 06.00 hours. No depth differences were observed. Phillip (1938) found that in the laboratory *Chironomus thummi* emerged in bright daylight and not at night. On the reservoirs during calm weather individuals of *Chironomus anthracinus*, *Cricotopus sylvestris* and *Psectrocladius limbatellus* were commonly seen emerging in full daylight. It is probable, however, that most of the chironomids entered the traps between 18.00 and 24.00 hours. Palmén (1955) found the peaks of emergence of species in 1-2 m. of brackish water to be around midnight.

It has been pointed out that an inaccuracy will be introduced in trapping if there is any lateral exchange of pupae between depth-zones owing to water movement, and one reason for placing the traps close to the bottom was to reduce the possible effects of this. Scott and Opdyke (1941), using floating traps, found a higher emergence per unit number of larvae in shallow water than in

deep, and suggested that an inshore migration of larvae or pupae might take place. There seems no doubt that pupae can be carried considerable distances by water movements before reaching surface traps. It is of importance to know, therefore, whether they might travel far before entering traps set about 1 m. above the bottom. Some data on pupal exuviae might seem relevant to this at first sight.

As has been said, the pupal skins of adults which emerge in the traps remain floating in the jars, but usually there are fewer skins than adults, some having sunk presumably because of fungal attack. At Kempton Park East Reservoir all the skins found were counted and Table V shows counts for six common species expressed as a percentage of the adults caught. The percentage recovery of skins in shallow water showed no marked difference from that obtained in the traps at 6.8 m. The lowest recovery of skins is found in the smallest species (*Cl. atridorsum*), the highest in the largest (*C. plumosus*).

TABLE V.—Total annual catches of adults and pupal skins of six common species caught in nine traps at Kempton Park East Reservoir in 1951. The counts of skins are expressed as percentages of trapped adults.

Species.	Adults caught.	Skins (%).
<i>Cladotanytarsus atridorsum</i> . .	4,234	10
<i>Psilotanytarsus rufovittatus</i> . .	7,401	13
<i>Tanytarsus holochlorus</i> . .	3,056	22
<i>Endochironomus albipennis</i> . .	767	27
<i>Procladius choreus</i> . .	13,098	28
<i>Chironomus plumosus</i> . .	694	46

Occasionally, however, more skins may be recovered than adults. At Staines South Reservoir, for example, the following catches were obtained from trap number 1 at 2 m.

TABLE VI.—Anomalous catches in Trap I at Staines South Reservoir.

Date.	Species.	Adults.	Skins.
16.vii.1951 . .	<i>Tanytarsus lugens</i>	4	142
	<i>Chironomus plumosus</i>	0	19
3.ix.1951 . .	<i>T. lugens</i>	0	32
	<i>C. plumosus</i>	1	21

Such catches are only recorded from traps in shallow water in wave-washed zones and are explained by the fact that the skins from midges emerging over the entire reservoir drift towards the shore, near which many are continuously circulated by the waves. Others are washed ashore and accumulate there in large conspicuous masses. It seems unlikely, however, that pupae are carried into submerged traps in this way as only a minute or less is spent at the surface by the living insect.

Nevertheless the possibility of the ascending pupae being carried in the layer of water 1 m. from the bottom must be given consideration, although in summer, when the reservoir shows slight thermal stratification, the movement may be assumed to be negligible.

The emergences of *Procladius choreus* (fig. 12) in the autumn of 1950 show high numbers from the side of the reservoir but very few from the floor. From 21st September to 30th October the mean wind direction was approximately south-west and the mean velocity was 10.5 km. per hour. The surface waters would be driven down-wind and a compensatory return current would therefore move over the floor of the reservoir and up the west side. That this would carry pupae arising from the profundal is, however, hypothetical and is, moreover, not borne out by the findings of the following year when, for example, on 13th and 14th September the mean wind velocity was 24.0 km. per hour, the stronger gusts being south-west, yet *Procladius* was nevertheless caught in fair numbers in the profundal traps.

It must be concluded that there is no concrete evidence that transportation of pupae in the lowermost metre of the water does take place. At present the anomalous emergences of *P. choreus* remain unexplained.

The emergence of *P. choreus* raises the important point that, in the interpretation of any emergence histogram, it is necessary to distinguish features of the population in the reservoir as a whole from features which are peculiar to the population on the sides. It is clear that, if egg-laying is random, midges which emerge from the littoral and sublittoral will oviposit over the entire water surface. Hence the progeny of adults which emerged from shallow water in spring may emerge in summer from the profundal along with the insects which overwintered there. From a temporal point of view, therefore, there is a mixing of faunas from different depth zones. In a very large reservoir, such as the Queen Mary Reservoir, the area of the floor is so much greater than that of the sides that the influence of such additions from the littoral can be ignored in the interpretation of the profundal emergences. In a small reservoir, however, account must be taken of these additions. In Kempton Park East Reservoir, for example, the sides down to 6 m. have an area of about 18 per cent. of the whole reservoir, and it is very likely, therefore, that some of the irregularities in the profundal emergences of species such as *P. choreus*, which begin to emerge in shallow water several weeks before they emerge from the profundal, are caused by additions of this nature. Not enough is known, however, of the fecundity of the chironomids or of the mortality of the offspring to make any detailed analysis of the histograms in terms of this factor. A general survey can only draw attention to its existence.

Occasions of faulty trapping were noted, records being kept of traps which were full of water on being lifted, and of catches which were lost or suspected of being lost in rough weather. No allowance is made in the histograms for low numbers resulting from these. The most frequent faults occurred in trap II 7, which gave low catches in July and the first half of August.

No visit was paid to Kempton Park East Reservoir on 29th September, 1950. A week's catch was therefore obtained from the traps when they were examined on 2nd October. No visit was paid on 6th September, 1951 to Staines South Reservoir. On 7th August, 1951 sampling on both reservoirs was a day overdue so that a five-day catch was obtained.

References to records of the species from other parts of the world have been largely omitted from the following treatment. These may be found in the works of Thienemann (1954) and Brundin (1949).

The following abbreviations are used :

K.P.E.R. : Kempton Park East Reservoir.

S.S.R. : Staines South Reservoir

Q.M.R. : Queen Mary Reservoir

Histograms of the Staines South Reservoir catches are given only where they show information not illustrated by the Kempton Park East Reservoir results.

In the Kempton Park East Reservoir histograms 6·8 m. (a), (b) and (c) correspond to traps 7, 8 and 9 in figure 3. In 1950 a single trap was set out on the last (easterly) buoy of line IIb, and when catches were obtained in it they are cited in the histograms as 6·8 m. (d). Similarly, in the Staines South Reservoir histograms trap 9 m. (e) is farthest from the shore.

2. *Tanypodinae*.

(1) *Pentaneura carnea*.—Though generally common, this species was found only once in the reservoirs, 1 female being caught on 7th August, 1951, at K.P.E.R.

(2) *Pentaneura falcigera*.—One male, 7th March, 1950, Q.M.R. Humphries (1938) found it as a rare spring species in the Grosser Plöner See.

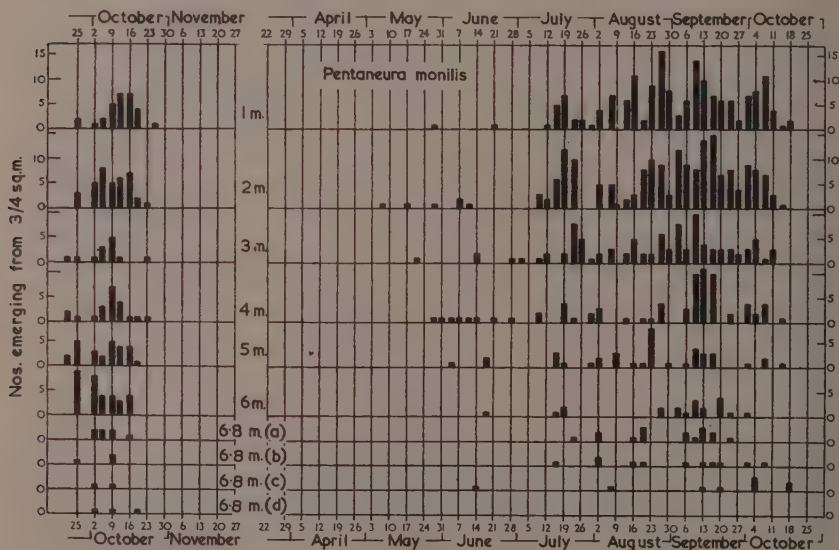


FIG. 9.—The emergences of *Pentaneura monilis* from Kempton Park East Reservoir.

(3) *Pentaneura monilis*.—Figure 9 shows the emergences of this species from K.P.E.R. The optimum depths are 1 and 2 m. and the histogram, although broken up, is interpreted as involving two generations, the population which survived the winter being small. Altogether 395 males and 407 females were

trapped. Judd (1953) found *P. monilis* to emerge from 18th May to 8th September from a marsh in Ontario. At S.S.R. the main catches were at 3 m. from 10th September to 8th October. A few individuals were caught at 9 m. (20th, 23rd August, 1st October), and this suggests that the species may occur in the profundals of eutrophic lakes.

(4) *Pentaneura ornata*.—One male, 4 females, 12th July, 1951; 1 male, 4 females, 7th August, 1951, all in swarms at K.P.E.R. The species seems to be rare in Britain (Edwards, 1929).

(5) *Pentaneura phatta*.—Three males, undated, from swarm, K.P.E.R.

(6) *Anatopynia notata*.—Single individuals were trapped on 24th May, 1951 (trap I 1), 31st May, 1951 (trap II 2), 18th June, 1951 (trap III 2); 2 males, 27th August, 1951, 1 female, 25th October, 1951, in swarms, K.P.E.R.

(7), (8) *Procladius choreus* and *Procladius crassinervis*.—The question arose as to whether or not *P. choreus* Meig. and *P. crassinervis* Zett. were distinct species, and examination of the literature raises the further question of the relationship to both of *P. culiciformis* L., usually treated as a variety of *P. choreus*.

Most of the specimens of *P. choreus* from K.P.E.R. fit Edwards' (1929) description, with "tarsal beard short but distinct". Johannsen (1905: 160) writes: "fore tarsi of the male bearded". Goetghebuer, however, states (1936: 10) "fore tarsus not bearded" and in Brundin's tentative key (1949: 812) to the Swedish species of the genus, *choreus* falls under "tarsal beard scarcely indicated or wholly absent". The beardless form may be regarded as the variety *culiciformis*. Edwards and Goetghebuer regard *P. culiciformis* with no beard, and hypopygium as in *choreus*, as a variety of *choreus*. Coe (1950) treats *culiciformis* as such but adds "possibly a distinct species".

Johannsen (1905, pl. 32, fig. 2) and Malloch (1915, pl. 28, fig. 5), however, figure for *culiciformis* a hypopygium distinct from that of *choreus*, the style having a long backward process. Morissey (1950) discusses the relationship between *choreus* and *culiciformis* and separates them using material collected from two different habitats. He found a continuous gradation in colour between the extremes described by Johannsen but the hypopygia were distinct and showed no gradation. In one form the arms of the style were nearly equal. This corresponded with Malloch's *culiciformis* and the males were never bearded. In the other the posterior arm was not produced and four out of ten of the males had the fore-tarsi bearded. This form resembled Malloch's *choreus*. The pupae, he adds, of the two species seemed identical. He, therefore, separates the two forms on the basis of the structure of the hypopygium.

The hypopygium, however, with processes of approximately equal length, attributed to *culiciformis*, has the same form as that of *P. crassinervis* Zett. (Coe, 1950: 132, fig. 183f), a dark slightly bearded species.

At S.S.R. nearly all the specimens of *Procladius* could readily be identified as *choreus* or *crassinervis*, although the antennal ratio (A.R.) of *crassinervis* was 2.2 whereas typically it is 2.5 (Edwards, 1929). At K.P.E.R., however, forms were commonly found which could not be called with certainty either *choreus* or *crassinervis* for the hypopygium, the coloration, and the beard were intermediate.

Specimens from both reservoirs were identified only as *choreus* or *crassinervis*, the *culiciformis* category not being considered. The doubtful ones were grouped with *choreus*, because at K.P.E.R. *choreus* was much more abundant and errors would, therefore, be swamped by the larger numbers. The total number of individuals of *choreus* caught at K.P.E.R. in 1951 was 13,098 and of *crassinervis* 1050. Errors would certainly be more numerous in the case of the females, as their identification depended only on colour characters, which tended to be lost when the insects were preserved. That this was so is shown by the following figures :

TABLE VII.—*P. choreus* and *P. crassinervis* at 3, 4, and 6·8 m.
in Kempton Park East Reservoir.

	Species.	Males.	Females.	Males as percentage of total.
Catches in traps 3 and 4 in 1951 .	<i>P. choreus</i>	1124	1747	39
	<i>P. crassinervis</i>	243	53	82
Catches in traps 7 and 8 in 1951 .	<i>P. choreus</i>	1378	1874	42
	<i>P. crassinervis</i>	253	56	81

Of the total of 13,098 individuals of *P. choreus* caught, 41 per cent. were males, i.e. the ratio of males to females was 1 : 1·48. The estimate of females will include the erroneously placed *P. crassinervis* specimens but, assuming a

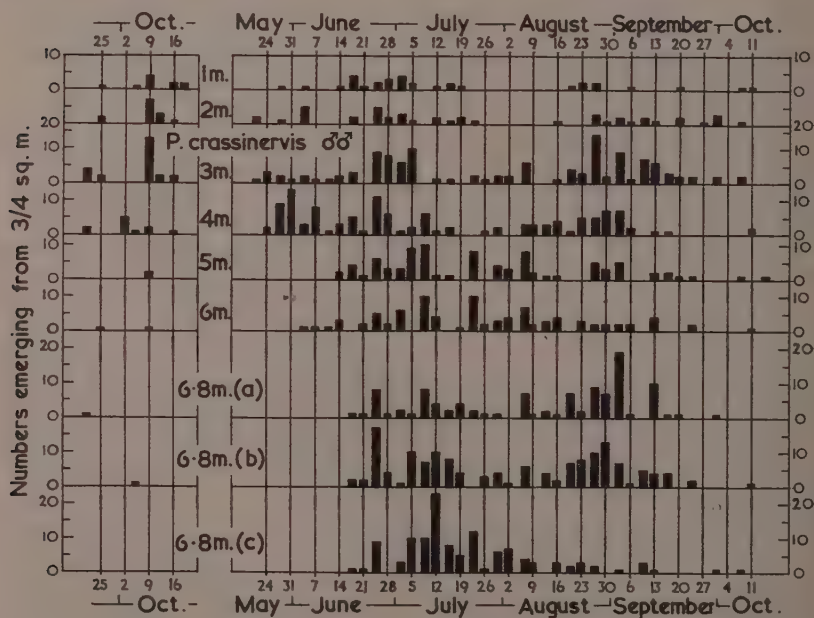


FIG. 10.—The emergences of males of *Procladius crassinervis* from Kempton Park East Reservoir.

sex ratio of 1:1.5 for *P. crassinervis*, these could not total more than 1127, for only 871 *crassinervis* males were caught in 1951 and 179 clearly distinguishable females. The above figures, therefore, show that a maximum of 1127, or 86 per cent. of the total number of females, was mistakenly grouped with *P. choreus*. This will not, however, significantly affect the emergence figures for *P. choreus* as it was at least six times as abundant as *crassinervis*.

The taxonomic possibilities are (1) that *P. choreus* and *P. crassinervis* are different species, reproductively isolated but morphologically nearly the same (sibling species), (2) that they are individual variants of one species, and (3) that they are subspecies, in which case, by definition (Mayr *et al.*, 1953) 75 per cent. of the individuals of one subspecies must be different from all other individuals of the other subspecies.

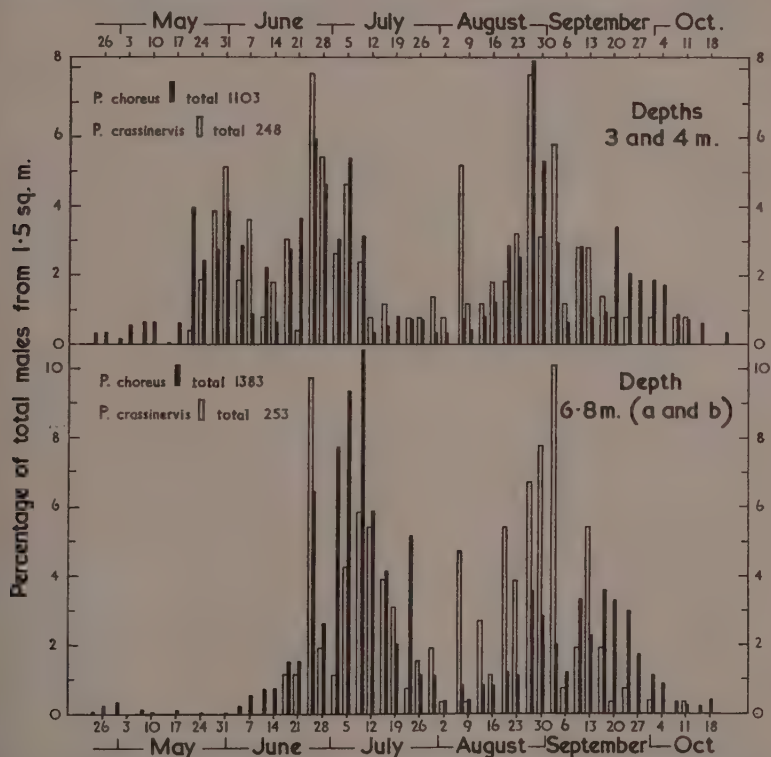


FIG. 11.—The emergences of the males of *Procladius choreus* and *P. crassinervis* from 3 and 4 m., and 6-8 m., expressed as percentages of the total numbers of each.

The presence of intergradation of characters in the two forms certainly suggests conspecificity, and, if the emergence curves of the two were found not to differ significantly, then they could both belong to one population.

In figure 10 the emergences of the males of *P. crassinervis* are plotted for each depth at K.P.E.R. Examination of these at 6-8 m. shows a bi-modal emergence

indicating two generations, although at 6.8 m. (c) the second is markedly reduced. On 7th August there is a conspicuous emergence from all depths below 2 m. The sampling period for this catch was five days, the previous catch having been removed from the traps on the 2nd, whilst the sampling period for all other catches was alternately three and four days. The high numbers caught on the 7th are, therefore, in part owing to this longer sampling period but not entirely, as is evident from the absence of a similar increase in *P. choreus*. The females of *P. crassinervis* gave a very similar emergence histogram.

The males of *P. crassinervis* are most abundant at depths of 3, 4 and 6.8 m. and emergences from these depths will therefore give the best comparison with those of *P. choreus*. Figure 11 shows the numbers of males of *P. choreus* and *P. crassinervis* which emerged from 3 and 4 m. taken together and from 6.8 m. (a) and (b) expressed as a percentage of the total. Examination of the emergences from 3 and 4 m. shows that there is no significant difference between the emergences of the two forms as a whole, but the numbers of *P. crassinervis* on 7th August cannot be explained on the grounds of random variation. The emergences from 6.8 m. show a close correspondence in the first generation. There is the marked increase of *P. crassinervis* on 7th August, and in the second generation the emergences differ. The mode for *P. crassinervis* is on 3rd September, whilst for *P. choreus* it is on 17th September (20th September if the males and females are considered together, see fig. 12). The low numbers for both forms on 6th September seem to be owing to loss of part of the catch, for low numbers were recorded also for *Chironomus plumosus* (fig. 19) and *Endochironomus albipennis* (fig. 25) but not, it must be noted, for *P. choreus* as a whole (fig. 12).

It is difficult to explain the discrepancy between the second generations of *P. choreus* and *P. crassinervis* at 6.8 m. It is clear that, if they correspond in shallow water, then the growth rates of the two species are the same. It would appear that the two forms belong to one population but that *crassinervis* arises at irregular times, for reasons which are unknown.

The catches of the two forms at S.S.R. were estimated in groups of 1-10, 11-20, 21-30, etc. Peak catches of both forms occurred on 7th August (five-day period) and 3rd September. The September catch supports the view that they belong to the same population.

No difference could be found between the pupae, and the larvae could not be compared, as no *crassinervis* adults were obtained from *Procladius* larvae. According to Johannsen (1937: 23) the larva and pupa of *P. culiciformis* are distinguishable from those of *P. choreus*. *P. culiciformis* is said to have eight or nine teeth in each paralabial comb and the pupa has about 30 spines on each terminal paddle; *P. choreus* has seven paralabial teeth and 35-40 spines (Johannsen, 1937, quoting Zavrel and Thienemann, 1921). These characters, however, must be very variable, for final instar exuviae of *P. choreus* larvae from K.P.E.R. have eight or nine paralabial teeth, of which the outermost may be very small, and the pupal paddles have 25-45 spines.

Lenz (1936: 73), dealing with the larvae of this genus, groups *choreus* and *culiciformis* as synonymous with each other.

The relationships of *P. choreus*, *P. culiciformis* and *P. crassinervis* are clearly in need of closer study. Brundin (1949: 687) considers *Procladius* to be one of the most difficult chironomid genera and claims that specific

boundaries can only be established on the basis of a revision of both pupal and adult material.

TABLE VIII.—Catches of five species of Chironomidae at Kempton Park East Reservoir.

<i>Procladius choreus</i> (during 1951).				<i>Psilotanytus rufovitatus</i> (during 1951).		
Trap.	Line I.	Line II.	Line III.	Line I.	Line II.	Line III.
1	520	765	305	432	323	70
2	542	824	367	334	386	58
3	459	534	690	258	315	215
4	284	440	464	119	89	125
5	155	304	180	89	119	73
6	134	301	74	146	183	38
7	476	80	202	676	42	55
8	1183	227	1084	785	209	396
9	844	539	1121	820	640	406
Total	4597	4014	4487	3659	2306	1436

<i>Chironomus plumosus</i> (during 1951).				<i>Cladotanytarsus atridorsum</i> (during 1951).		
Trap.	Line I.	Line II.	Line III.	Line I.	Line II.	Line III.
1	0	0	0	155	139	38
2	0	0	0	69	689	151
3	0	0	2	75	256	776
4	21	36	88	324	174	567
5	36	18	25	43	342	117
6	51	43	50	50	195	37
7	47	16	46	5	3	1
8	50	41	54	6	0	2
9	25	26	19	7	8	5
Total	230	180	284	734	1806	1694

<i>Tanytarsus holochlorus</i> (during 1950 and 1951).						
Trap.	1950			1951		
	Line I.	Line II.	Line III.	Line I.	Line II.	Line III.
1	4	0	1	10	7	0
2	6	2	14	9	27	2
3	75	39	29	16	100	100
4	209	306	264	97	93	378
5	106	128	112	61	309	340
6	9	32	24	27	108	23
7	0	1	0	164	18	56
8	0	0	0	126	68	265
9	0	0	0	119	213	303
Total	409	508	444	629	943	1467

Figure 12 shows the emergences of *P. choreus*. It was the most abundant species trapped at K.P.E.R. and was found at all depths in S.S.R. Table VIII shows the variability of the total catch from K.P.E.R. for 1951. The low figure for trap II 7 is attributed to faulty sampling. Trap II 8 has likewise certainly been at fault, although this was not apparent at the times of sampling.

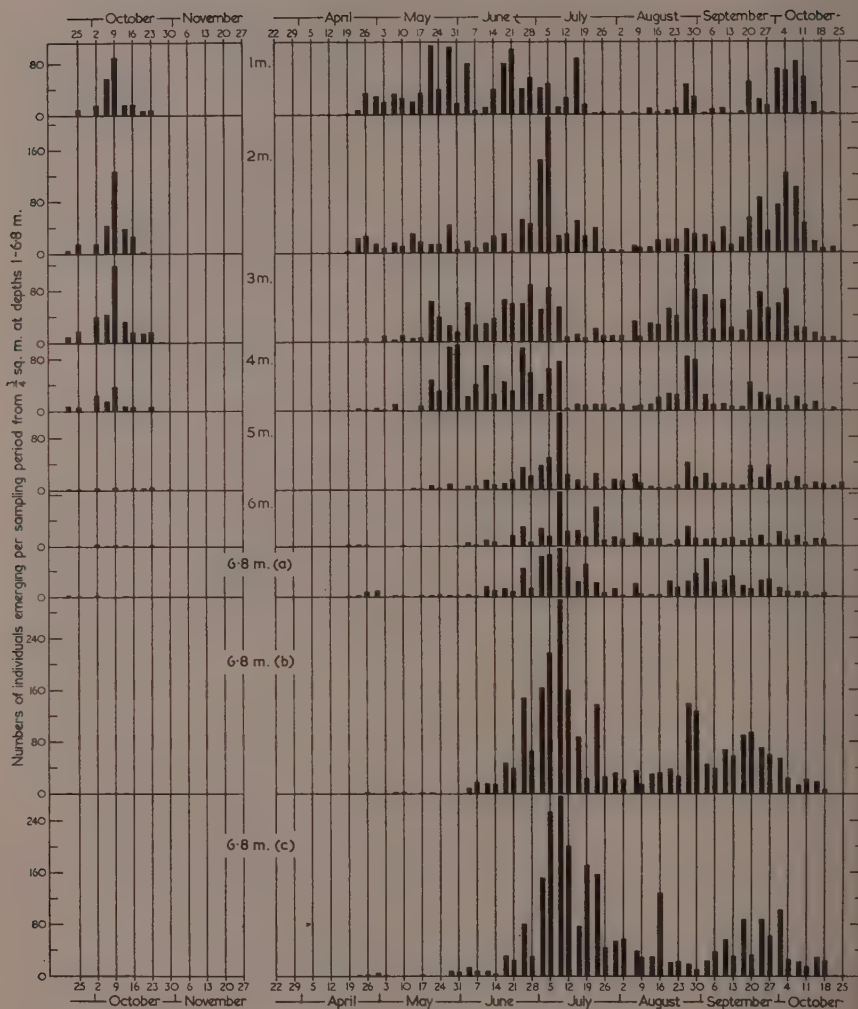


FIG. 12.—The emergences of *Procladius choreus* from Kempton Park East Reservoir.

The profundal population begins to emerge as early as the third week in April and continues to the end of October. The distribution here is clearly bi-modal, indicating two generations per year. Conspicuous irregularities occurred on 16th August at 6-8 m. (c) and again on 27th and 30th August at 6-8 m. (b). The most likely cause seems to be insects which hatched from eggs laid by females which emerged early in the year from the littoral.

P. choreus is one of the most characteristic macroscopic animals of the profundal of eutrophic lakes. It is bi-voltine at 6-8 mm. in K.P.E.R. That it has

two generations a year in shallow lakes is suggested by data from various sources (Lindeman, 1942a). From figure 8 it is seen that the modes of the two profundal emergences (10th July, 20th September) are separated by 1230 day-degrees.

Borutzky (1939b) found that *Tanytus* had two generations per year at depths 4–13 m. in Lake Beloie, but more in the littoral, depending on the temperature. In K.P.E.R., however, the polymodal distribution at 1 and 2 m. cannot be taken as four consecutive generations because the summer temperature differences between the littoral and profundal amount to only 100 day-degrees. The interpretation of the catches at 1–4 m. is made difficult by the fact that it is not known to what extent fish predation has influenced them. Moreover, as has been pointed out (p. 171), it is not justifiable to trace the sequence of emergences at one depth independently of what is taking place at other depths, as insects emerging from any particular zone may lay their eggs in other zones. The emergences in the littoral are, therefore, taken to involve basically two generations. The emergence of insects derived from eggs laid in 1950 is completed by 26th July, the emergence of eggs laid in 1951 by 25th October or later.

The emergences, however, are certainly more complicated than this. It is remarkable that during October 1950 the numbers of *P. choreus* trapped in the profundal amounted to only a few individuals (fig. 12), whilst fair numbers were caught at 1–4 m. These facts are clearly of significance, but are difficult to explain. If, as seems likely, the possibility of water movements affecting the trapping can be ruled out (p. 171), then the absence of an emergence from the profundal must be taken as real. A possible explanation of the data is that the second generation of *P. choreus* had completed its emergence from the reservoir by the

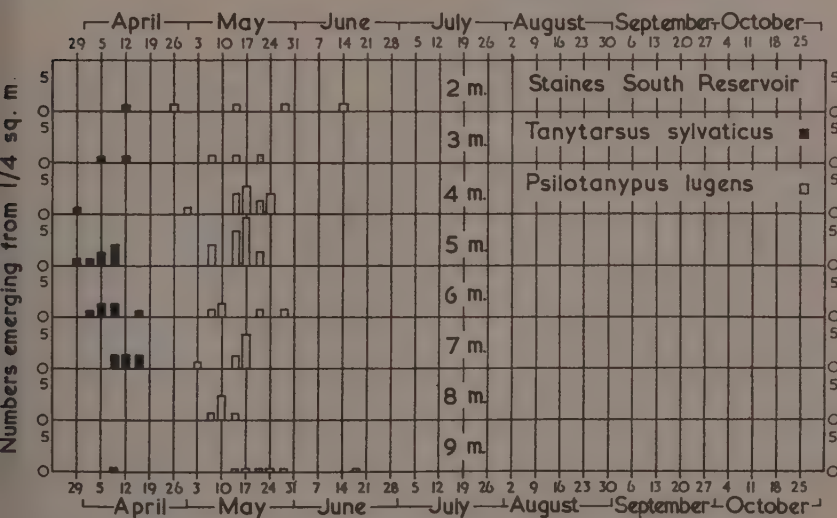


FIG. 13.—The emergences of *Psilotanytus lugens* and *Tanytarsus sylvaticus* from Staines South Reservoir.

third week in September and the insects emerging from 1-4 m. after that date are a third generation. This, however, remains hypothetical.

Probably all tanypodinid larvae are free-living predators. Their feeding has been studied by Zavrel (*in* Zavrel and Thienemann, 1916) and Morgan (1949). Newly hatched chironomid larvae, tubificids, Cladocera, Copepoda, and Ostracoda are eaten. The relative importance of zooplankton to plant-eating chironomid larvae (*i.e.* *Tanytarsus*) as food for *P. choreus* and other carnivorous species requires investigation.

(9) *Psilotanypus lugens*.—This species was found only at S.S.R., where it is present at all depths, with an optimum at 5 m. It is univoltine, emerging in May (fig. 13). Little seems to be known about it. It is recorded from a Lancashire tarn (Macan, 1949).

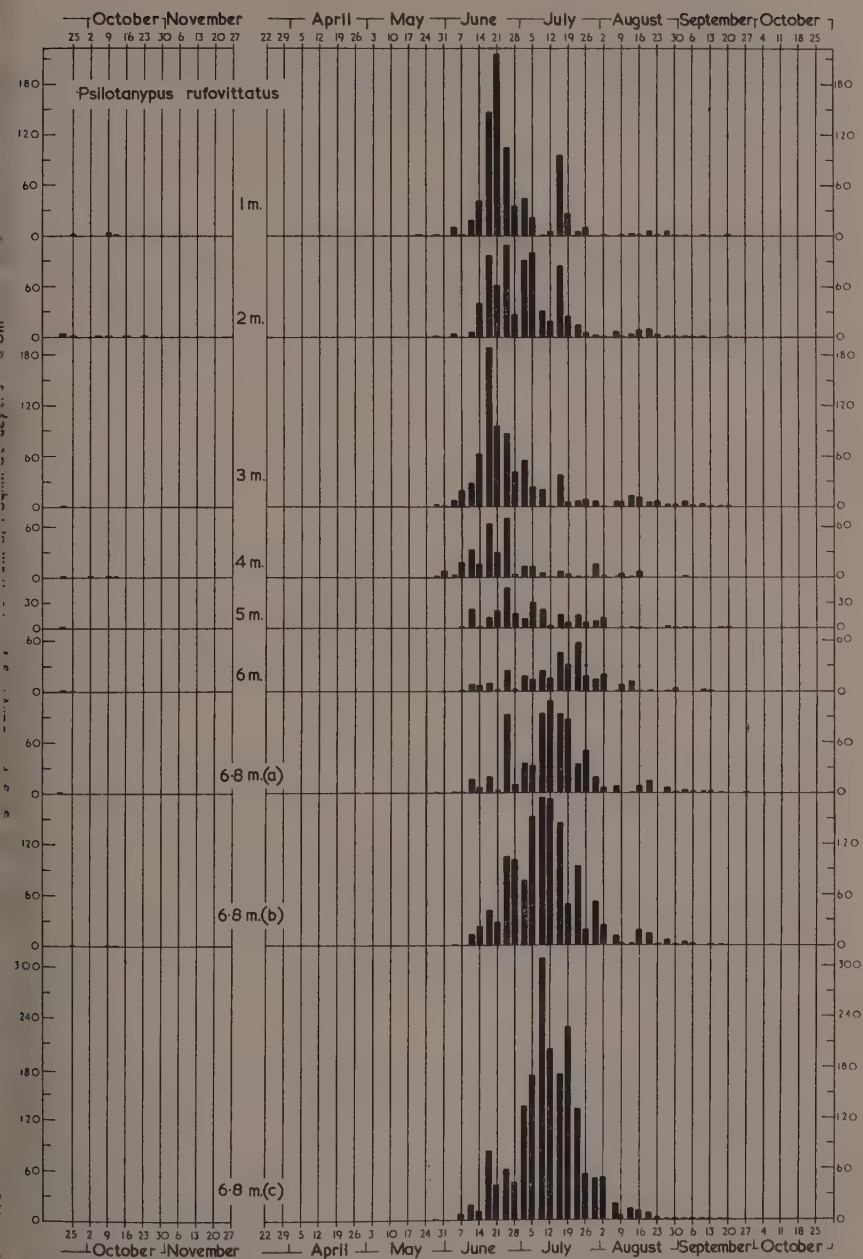
(10) *Psilotanypus rufovittatus* is an abundant univoltine species found at all depths in K.P.E.R. and S.S.R. (fig. 14). The total catches in each trap at K.P.E.R. in 1951 are shown in Table VIII. The standard deviation of the distribution of the emergences at 6.8 m. (c) in K.P.E.R. was found to be 15.0 days by the method of plotting the cumulative frequencies on probability paper. The sampling period was taken as 3.5 days (the average of the alternate periods). A full statistical calculation from the same data gives an S.D. of 12.9 days. A test of kurtosis on the 6.8 m. (c) emergences showed that the distribution is significantly peaked (leptokurtic β_2 3.84) and is significantly skewed (β_1 0.03, for 1856 observations).

The mode at 1 m. was 21st June and at 6.8 m. about 12th July. The last date on which the reservoir was isothermal was 17th May. From this date until the mode at 1 m. 500 day-degrees had accumulated, and from 17th May until the mode at 6.8 m., 850 day-degrees had accumulated.

In shallow water (1-3 m.) a second peak arose a week after the main emergence was completed. This was also found for *Psilotanypus* sp. by Miller (1941 : 38) in Costello Lake, Ontario, at depths of 1-17 m. One possible explanation for such bi-modal emergence distributions is that a certain proportion of the larval population enters diapause whilst the remainder does not, in accordance with a response to changing photoperiod (*cf.* Corbet, 1955).

In S.S.R. the mode at 2 m. was 25th June and was the same at 6 m. At 7 m. it was 28th June. The differences between temperatures on the bottom at 3 m. and 6.8 m. in the two reservoirs were the same in June, *i.e.* between 0.5 and 1.0° C.; nevertheless there was a delay of 17 days in emergence from 6.8 m. in K.P.E.R., but of only three days in S.S.R. Miller (1941) records that *Psilotanypus* sp. emerged simultaneously from 1 m. to 17 m. and suggests that the species migrates at random on the bottom and therefore all the individuals receive the same amount of heat. Temperature differences, however, cannot explain the difference between the dates of emergences in the two reservoirs. It may be of significance that if, as seems quite likely, the S.S.R. population is transported haphazardly by the water movements at the south-east corner, whilst the K.P.E.R. population on the west side is much less frequently disturbed, then the S.S.R. larvae would receive more light than do the K.P.E.R. larvae.

At K.P.E.R. 3293 males and 4108 females were trapped in 1951, the sex ratio therefore being 1 : 1.247.

FIG. 14.—The emergences of *Psilotanytus rufovittatus* from Kempton Park East Reservoir.

P. rufovittatus is recorded from the Grosser Plöner See (Lenz, 1936). The larval feeding habits are probably similar to those of *P. choreus*.

The respiration of the tanypodinid larvae has been little studied. Since they are free-living, they are presumably less influenced by the micro-stratification of oxygen in bottom deposits than case- or tube-forming species (Brundin, 1951). They are certainly tolerant of a wide range of oxygen conditions.

3. *Orthocladiinae*.

(1) *Orthocladus flexuellus*.—Two males, 28th June, 1951, from swarm, K.P.E.R. It is probably mainly a shallow-water inhabitant, but Laurence (1953) records it from cow dung.

(2) *Orthocladus glabripennis*.—Two males, 23rd February, 1950, Q.M.R.; 15 males, 7th March, 1950, Q.M.R.; 1 female, 26th November, 1951, K.P.E.R.; 2 males, 1 female, 17th March, 1952, K.P.E.R.; all from swarms.

(3) *Chaetocladus perennis*.—One male, 5th April, 1951, from swarm, K.P.E.R.

(4) *Chaetocladus piger*.—Three males, 2 females, 5th April, 1951, from swarm, K.P.E.R.

(5) *Dactylocladus semivirens*.—Frequently found in small numbers at K.P.E.R., but not trapped. Adults caught from swarms from 21st May, 1951 to 23rd August, 1951. The larvae build tubes of sand (Pagast, 1933 : 299 ; Thienemann, 1944 : 623). Humphries (1938) found them in the Grosser Plöner See "in very shallow water with a pure sandy bottom". It is almost certain, therefore, that in the reservoir the species occurs in depths of less than 1 m. and was therefore not trapped.

(6) *Diplocladus cultriger*.—Two males, 5th April, 1951, from swarm, K.P.E.R.

(7) *Psectrocladius barbimanus*.—Five males and 3 females were trapped from 1, 2 and 3 m. between 23rd April and 21st May, 1951, at K.P.E.R.

(8), (9) *Psectrocladius limbatellus* Holmgr. and *Psectrocladius stratiotis* Kieff. were separated on the basis of the antennal ratio and scutellum colour, using Edwards' key (1929). The *stratiotis* specimens were smaller than those of *limbatellus*, the imagines lighter, and the pupae had 28–37 hollow hairs on the paddle, whilst in *limbatellus* there were 33–48. Wülker (1956), who has examined some of the reservoir material, is of the opinion that it consists of only one species, i.e. *limbatellus*, and that the number of hairs on the paddle varies with body size.

The emergences of the specimens, identified as two species, are shown in figure 15. The *limbatellus* form arises in spring and autumn, the *stratiotis* form in summer. Probably only two generations are involved in the *stratiotis* emergences and the irregularities are due to the feeding activities of fishes (cf. *Cladotanytarsus atridorsum* at 1 and 2 m., fig. 30). At S.S.R. similar distributions were obtained and individuals of the *stratiotis* form were caught at all depths. In 1951, at K.P.E.R., 175 males and 512 females of *P. limbatellus* were caught, giving a male to female ratio of 1 : 2.9. In 1950, 39 males were caught and 129 females, giving a ratio of 1 : 3.3. In 1951, 101 males of *P. stratiotis* were caught

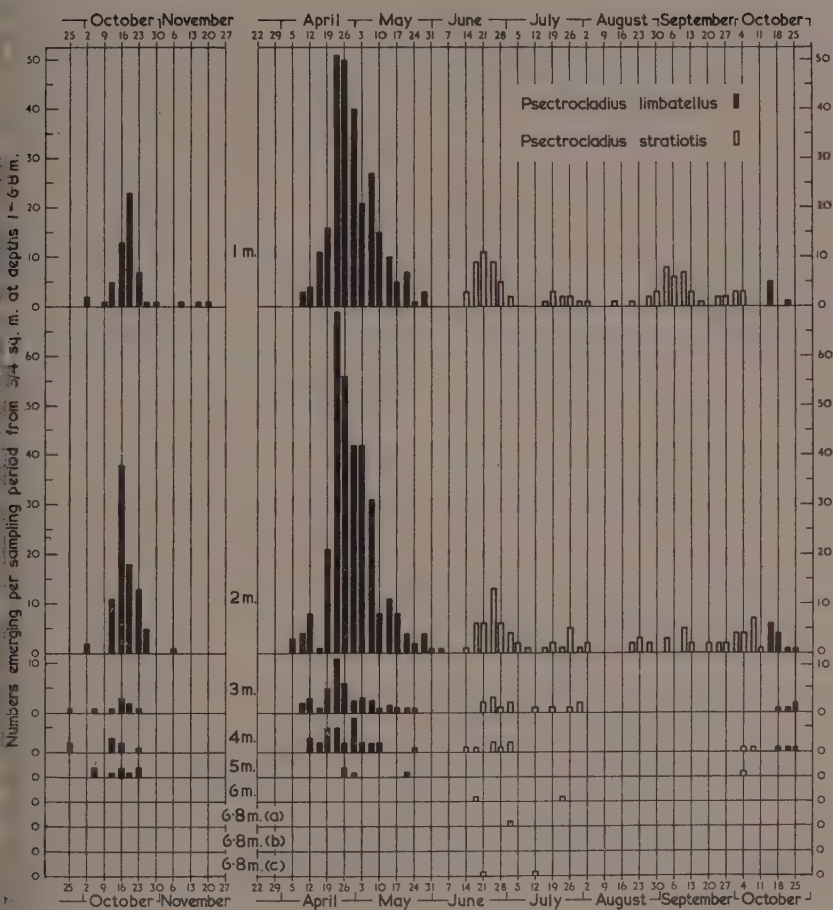


FIG. 15.—The emergences of *Psectrocladius limbatellus* and *P. stratiotis* from Kempton Park East Reservoir.

at K.P.E.R. and 103 females, giving a ratio of 1 : 1. Little is known of the feeding habits of *Psectrocladius*. The larvae probably feed on *Cladophora* and the organisms living on its filaments.

(10) *Cricotopus sylvestris*.—The emergences are shown in figure 16 and are interpreted as involving three generations per year. At S.S.R. the first generation was scarcely recorded, a few individuals only being caught from 2 m. on 31st May. The second and third generations had modes at 2 and 3 m. on 19th July and 10th September. In K.P.E.R. individuals were caught at 6-8 m. in August and September. These have been named *Cricotopus* sp. in figure 16, as there

may be some doubt as to their identity. At S.S.R., however, *C. sylvestris* was caught in small numbers at 7 m. from 16th July until 20th September and occasional individuals were caught at 8 m.

C. sylvestris is cosmopolitan and occurs in flowing as well as standing waters. The larvae live in tubes on the undersides of the leaves of aquatic plants such as *Potamogeton*, or they may build them in mud rich in algal debris. They abound in the *Cladophora* at the margins of eutrophic lakes, and are therefore especially numerous in hot calm summers when the alga develops as a dense mat extending several metres from the shore. If wave action is strong, however, and the *Cladophora* is broken up, then the larval population is reduced. This would seem to be the explanation for the great difference between the emergences in the autumns of 1950 and 1951.

(11) *Cricotopus bicinctus*.—Males were caught in small numbers swarming at K.P.E.R. on 21st May, 1951 and throughout June. Miller (1941) found it with an optimum depth at 7 m. in Costello Lake, where it appears to have one generation each year.

(12) *Cricotopus dizonias*.—The emergences are shown in figure 16 and probably involve three generations. At S.S.R. the modes of these at 2 and 3 m. were on 10th May, 12th July and 13th September. Fair numbers emerged from 7 m. and one individual was caught at 9 m. At K.P.E.R. the numbers (333 males and 496 females) emerging from 21st September to the end of October at 1 m. in 1950 were 40 times those of the same period and depth in 1951. This is attributed to the greater development of *Cladophora* in 1950. The species is characteristic of eutrophic lakes.

(13) *Cricotopus triannulatus*.—Males and females were caught from 1st to 21st June, 1951, from swarms at K.P.E.R.

(14) *Cricotopus trifascia*.—A few males were caught swarming at K.P.E.R. on 21st May, 1951. The larva is recorded from rivers (Humphries, 1951).

(15) *Nanocladius bicolor*.—One male trapped, 12th July, 1951, K.P.E.R., (trap III 1); 1 female, 28th June, 1951, in swarm, K.P.E.R.

(16) *Limnophyes* incert.—A single male trapped, 27th November, 1950, K.P.E.R. (trap II 1) was probably *L. pusillus* Eaton, but the terminal point of the style was slightly produced and there were five hairs to the squama. *L. pusillus* is semi-terrestrial (Strenzke, 1951). Meuche (1939) describes *L. minimus* Meig. as a typical autumn form of the *Cladophora* zone. The relationship of the two species is in need of re-examination (Strenzke, 1951 : 246).

(17) *Smittia atterrима*.—One male, 28th June, 1951, 6 males and 4 females 4th October, 1951, all from swarms, K.P.E.R. This species is commonly found in soil (Strenzke, 1951 : 255). Laurence (1953) found it in cow dung. It is almost certain, therefore, to have come from the pasture surrounding the reservoir.

(18) *Smittia contingens*.—Three males, 7th March, 1950, from swarm, Q.M.R. Recorded by Laurence (1953, 1954) from cow dung. Hall (1949) found swarming adults near a brackish stream. The species may be the same as *Euphaenocladius aquatilis* Goetgh. (Strenzke, 1951 : 254).

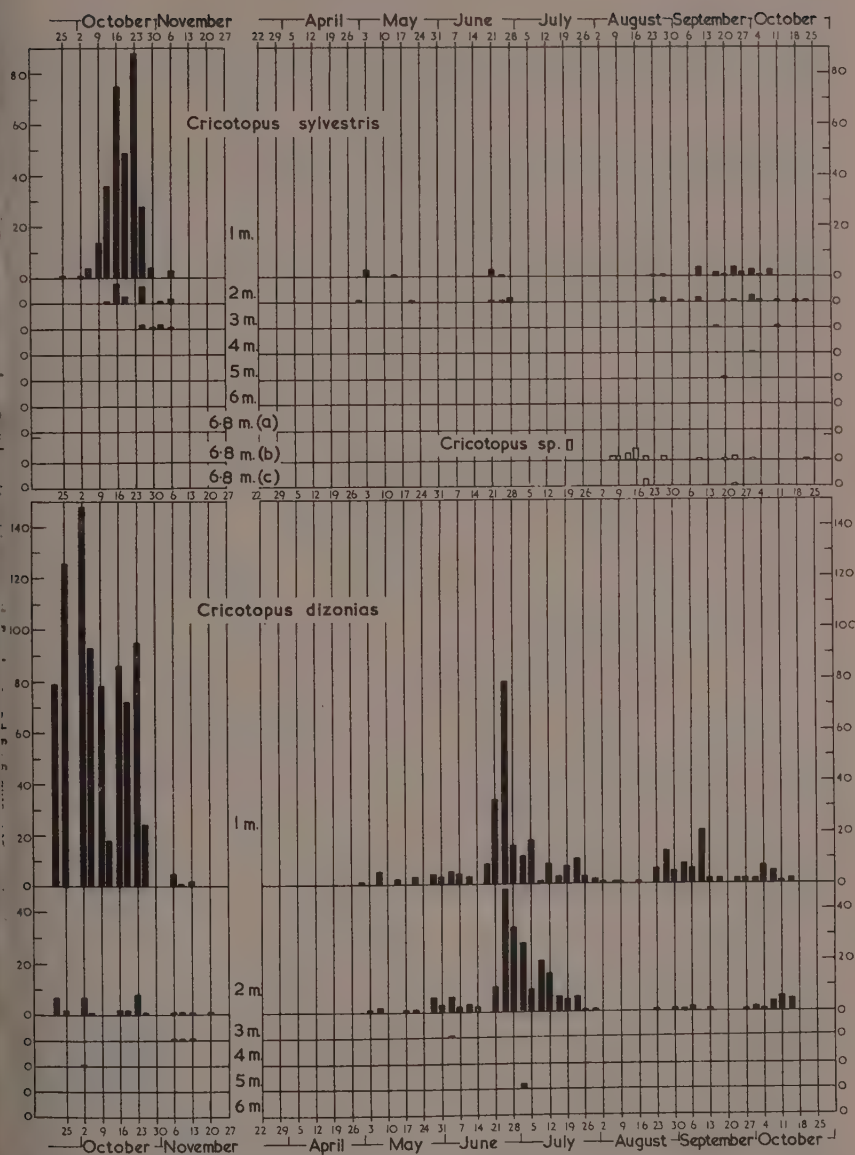


FIG. 16.—The emergences of *Cricotopus sylvestris*, *Cricotopus* sp. and *C. dizionias* from Kempton Park East Reservoir.

(19) *Smittia pratorum*.—One male, 1 female, 23rd August, 1951, from swarm, K.P.E.R. This species is recorded emerging from 3 m. in a Lancashire tarn in May (Macan, 1949).

(20) *Thienemanniella majuscula* (?).—One male, 28th May, 1951, 1 male 28th June, 1951, both from swarms, K.P.E.R.

(21) *Diamesa gaedii*.—Found from May to October in swarms at K.P.E.R.

4. Chironominae.

(1) *Pseudochironomus prasinatus*.—Fifty-one males and 34 females were trapped at K.P.E.R. but none was found at S.S.R. The emergences are shown in figure 17. There is probably only one generation each year. The species is a well-known summer form, flying from the end of May to September. Lenz (1937) discusses its ecology. It occurs commonly in stony algal-covered littorals. In Windermere it is found down to 9 m. (Humphries, 1936).

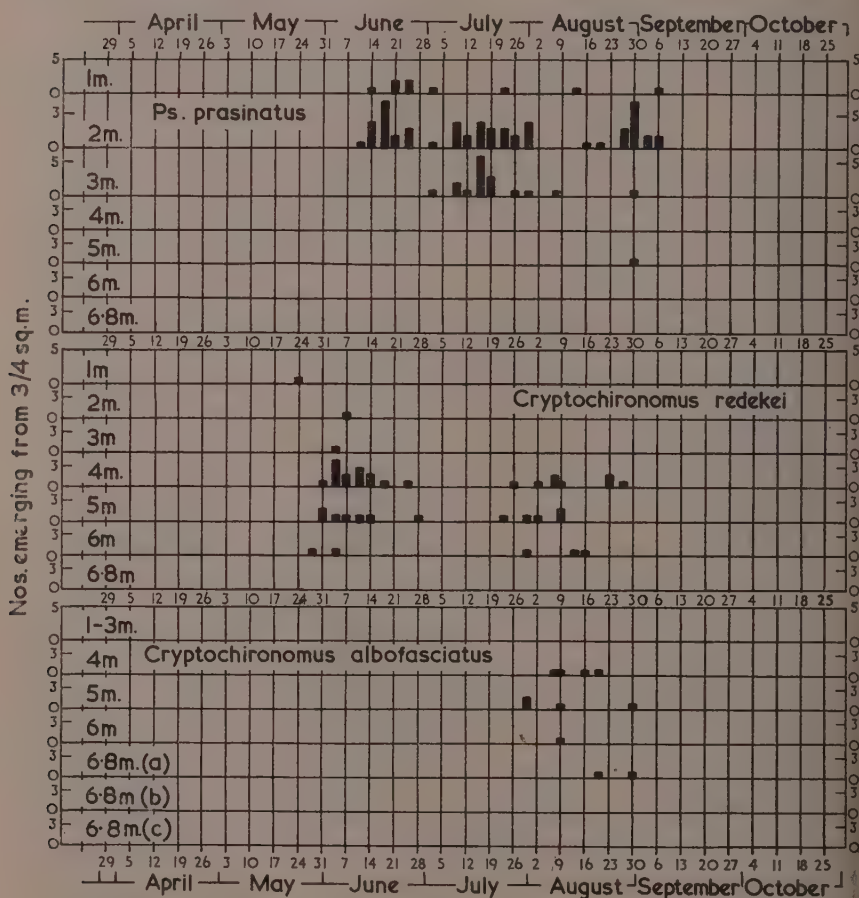


FIG. 17.—The emergences of *Pseudochironomus prasinatus*, *Cryptochironomus redekei* and *C. albofasciatus* from Kempton Park East Reservoir.

(2) *Chironomus anthracinus*.—This species was trapped at S.S.R. and caught in dense swarms in April at Q.M.R. but not one individual was found at K.P.E.R. It is one of the commonest species of the profundal at S.S.R. and emerges in spring (fig. 18). Emergence started in S.S.R. when the water was 6.5° C. Jónasson (1954) found a four-week emergence period with a mode on 10th May, 1954, for *C. anthracinus* in the profundal of Esrom Lake. Thienemann (1951b) records variations in the time of year when *C. anthracinus* swarmed at the Grosser Plöner See from 1918–50. On 20th September 1951, 20 males were caught in a swarm at S.S.R. Nevertheless most of the population is univoltine. Rempel (1936) found that a species which he called *C. hyperboreus* Staeg. has a two-year cycle. Townes (1945 : 130) writes that this is *C. anthracinus*, but Thienemann (1954 : 285) points out that Rempel's species belongs to the *plumosus* group of larvae and is neither *C. anthracinus* nor *C. hyperboreus*. Thienemann calls it *C. rempelii*.

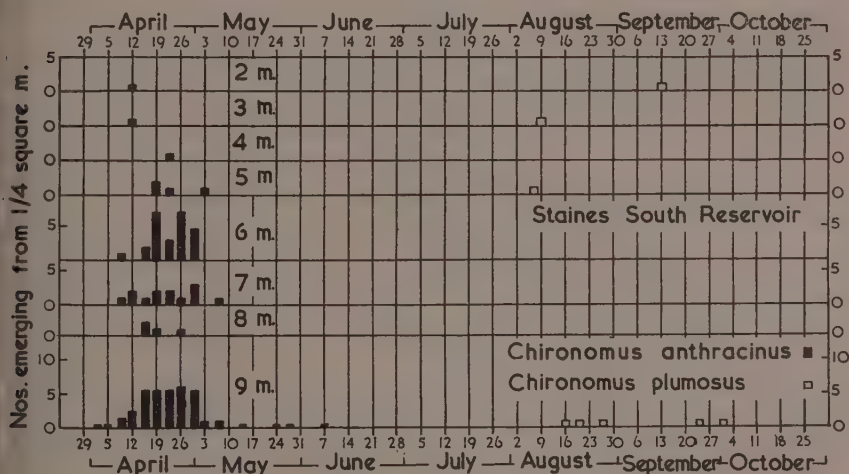


FIG. 18.—The emergences of *Chironomus anthracinus* and *C. plumosus* from Staines South Reservoir.

Berg (1938) gives a general account of the biology of *C. anthracinus*. It is one of the most characteristic species of the profundals of strongly eutrophic lakes. Lundbeck (1926) studied its distribution in the Grosser Plöner See. Walshe (1951b) made observations on its feeding habits. The larvae appear to live on detritus, and do not build U-tubes or use a filter-feeding mechanism.

C. anthracinus is commonly taken as an indicator of low oxygen conditions, although it is regarded as being more sensitive to them than *C. plumosus* (Brundin, 1951). Its total absence, however, during the survey, from K.P.E.R., where oxygen conditions are more favourable than at S.S.R., shows that this is not necessarily so. It is probably a nutritional rather than a respiratory quality of the deposits at S.S.R. that favours the dense numbers of *C. anthracinus* there.

(3) *Chironomus cingulatus*.—Trapped on four occasions in 1951 at K.P.E.R. (23rd April, 1 male (trap I 4); 26th April, 1 male (trap III 3) and 3rd May, 1 male (trap III 4)). The larvae are commonly found in ponds and pools but also occur in lake littorals.

(4) *Chironomus plumosus*.—The emergences are shown in figures 18 and 19. The S.S.R. catches give no indication of the very high numbers which emerged

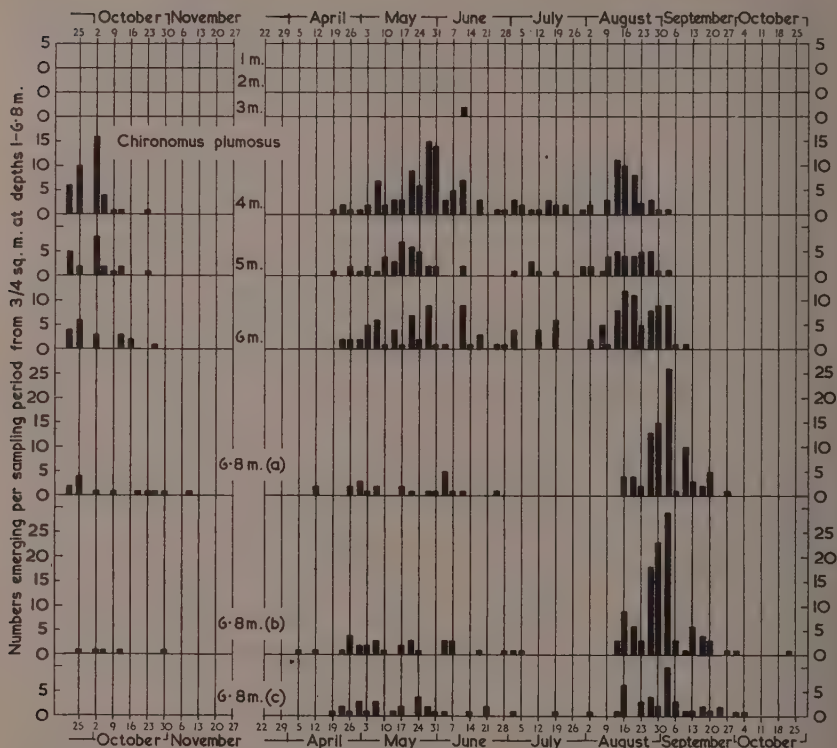


FIG. 19.—The emergences of *Chironomus plumosus* from Kempton Park East Reservoir.

during August and September (see p. 170). Table VIII shows the variation in the total catches at K.P.E.R. In 1951, 373 males and 321 females were caught; in 1950, 44 males and 53 females.

The species has two generations a year in shallow waters and one in deep (Borutzky, 1939a, Johnson and Munger, 1930). Lindeman (1942a) found evidence of a third generation in Cedar Bog Lake. The following calculation

from the emergences at 4 m. gives an estimate of the developmental threshold :

2nd October to 31st May . 1650 day-degrees and 241 days.

31st May to 23rd August . 1350 day-degrees and 84 days.

This gives a temperature of 1.9° C. for the developmental zero. The optimum depth was 4 m. for the winter generation, but there was no marked optimum for the summer one. The almost total absence of the larvae above 4 m. is probably due to the shallowness of the mud, which prevents tube-formation.

Chironomus plumosus is probably the best known of all chironomids and references to it abound in the literature (see Townes, 1945 : 132-3). Borutzky (1939a), Lundbeck (1926) and Johnson and Munger (1930) give accounts of its biomass relations in different lakes. The feeding habits are described by Walshe (1951b). The larva builds a U-shaped tube and uses a filter-feeding mechanism. *C. plumosus* is commonly accepted as being the chironomid species most tolerant of anaerobic conditions. Lindeman (1942b) has shown that the larvae in a mixed population can survive 120 days of anaerobiosis at 0, 5 and 10° C.; their ability to do this is bound up with their use of haemoglobin (Walshe, 1950 ; Walshe-Maetz, 1953).

(5) *Chironomus riparius*.—Caught in June and October in swarms at K.P.E.R. This is *C. thummi* Kieff., the adults of which must be separated from those of *C. dorsalis* Meig. on biometric grounds (Acton, 1955). It occurs most abundantly in polluted waters.

(6) *Limnochironomus lobiger*.—The emergence of this species from K.P.E.R. is shown in figure 20. Specimens were caught swarming at K.P.E.R. from 1st June until 12th July. It was not found at S.S.R. It is recorded with two emergence periods from Three Dubs Tarn in Lancashire (Macan, 1949).

(7) *Limnochironomus nervosus*.—Figure 20 shows the emergences from K.P.E.R. There is little doubt that seven females trapped at 2 m. from K.P.E.R. on 7th June and identified as *L. pulsus* were in fact *L. nervosus* (cf. emergences for *L. pulsus*). In 1951, at K.P.E.R., 130 males were trapped and 146 females. The emergences are interpreted as three generations per year. In S.S.R. most specimens were trapped about 13th September and two were taken at 7 m. The species is common and widespread. It lives in littoral muds, in algal mats, in reed beds and on stone substrata. It occurs in Windermere down to 6 m. (Humphries, 1936), in Three Dubs Tarn (Macan, 1949), and in the Grosser Plöner See (Humphries, 1938).

(8) *Limnochironomus pulsus*.—The emergences from K.P.E.R. are shown in figure 20. In 1951, 235 males and 274 females were caught. At S.S.R. *L. pulsus* was most abundant at 4 m.; one individual was caught at 8 m. This is the least sensitive of the *Limnochironomus* species in its temperature and food requirements. It occurs (with *L. nervosus*) in the highly eutrophic Väcksjö Lake (Brundin, 1949) and in the Grosser Plöner See.

(9) *Cryptochironomus albofasciatus*.—The emergences from K.P.E.R. are shown in figure 17. It was trapped at 3, 4 and 5 m. at S.S.R. from 23rd August to 20th September. The larva is probably a predator.

(10) *Cryptochironomus biannulatus*.—A single male was trapped in August

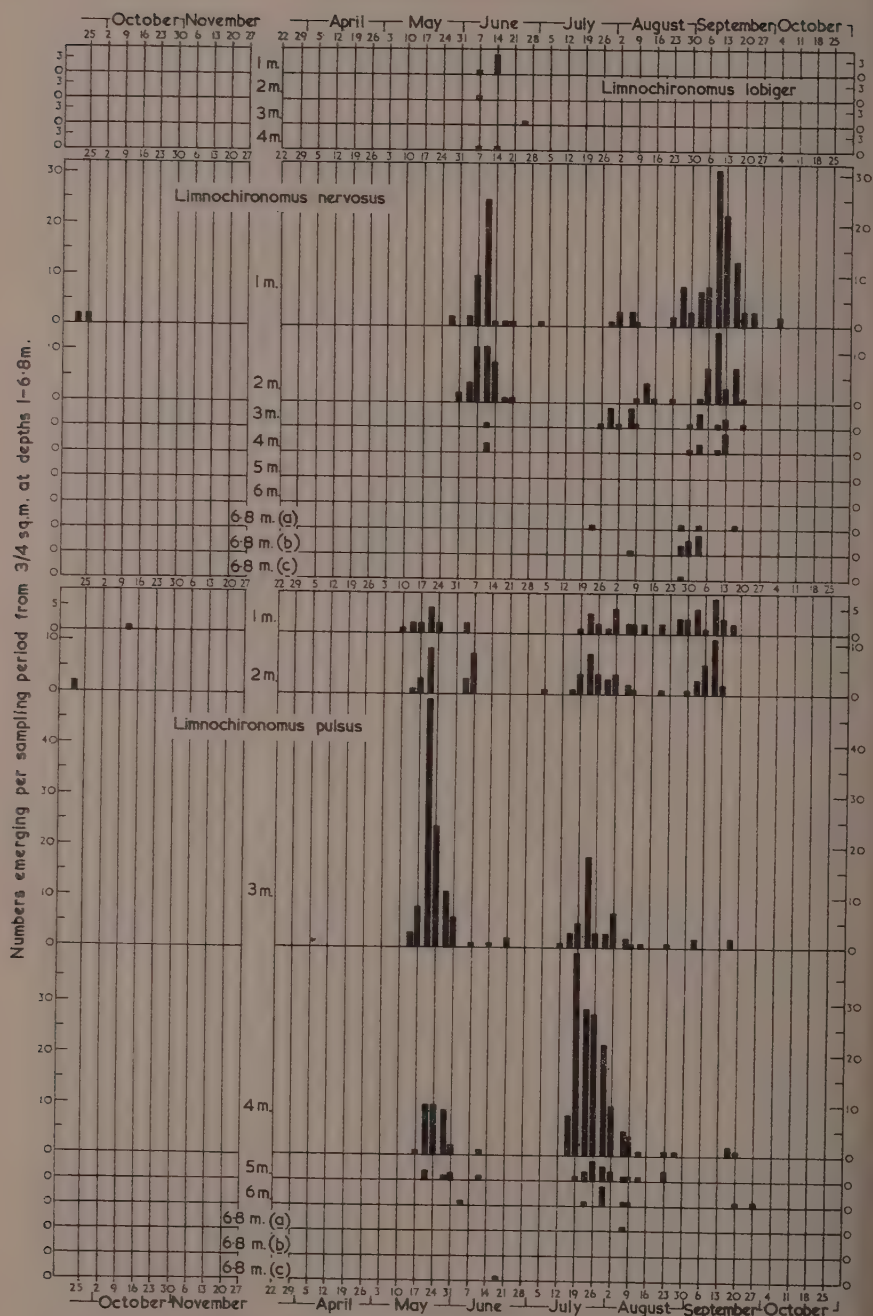


FIG. 20.—The emergences of *Limnochironomus lobiger*, *L. nervosus* and *L. pulsus* from Kempton Park East Reservoir.

at K.P.E.R. and mistakenly grouped with *C. albofasciatus*. Consequently the date and depth of trapping are not known. Meuche (1939) found this species in dead *Typha* reeds in Holstein.

(11) *Cryptochironomus psittacinus*.—Only 2 males were obtained from K.P.E.R.; 1 on 16th August, 1951, with a sweep-net, the other emerged on 24th August, 1951, in a rearing tank from mud taken from the littoral. This is *C. stylifera* Joh. and is recorded by Lindeman (1941) in Cedar Bog Lake and by Eggleton (1931) in the Third Sister Lake (6–10 m.).

(12) *Cryptochironomus redekei*.—This species, which was identified by Mr. P. Freeman, is new to Britain. It was found only at K.P.E.R. The emergences are shown on figure 17. Fifteen males and 28 females were trapped. The species was first found in Holland (Kruseman, 1933a), where it occurs in brackish water. It is also known in Finland (Storå, 1937). It is possible that some of the individuals represented in figure 17 are *C. psittacinus*, as *C. redekei* was confused at first with this species.

(13) *Cryptochironomus supplicans*.—Five males were trapped at S.S.R. at depths 2, 3 and 4 m., from 23rd August to 20th September, 1951. This species is found in the Grosser Plöner See (Humphries, 1938) at 1 m. in gravel and sand. It is fairly frequent in the South Swedish oligotrophic lakes (Brundin, 1949).

(14) *Cryptochironomus vulneratus*.—Only 2 males were found. Both were trapped at K.P.E.R.; 1 on 19th July at 6 m., the other on 30th August, 1951, at 4 m. The larva lives free in sand (Pagast, 1932). It probably feeds, at least in part, on oligochaets by sucking out their body contents (Thienemann, 1954 : 59).

(15) *Parachironomus vitiosus*.—The emergences of this species are shown in figures 21 and 22. There appear to be two generations a year in shallow water

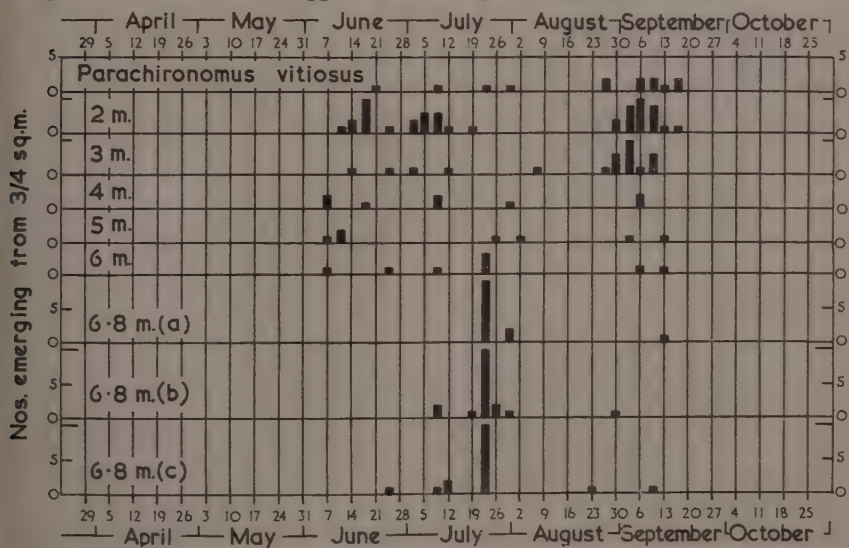
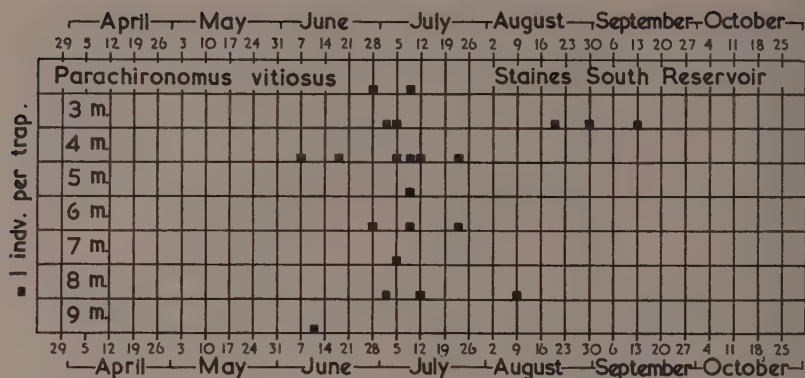
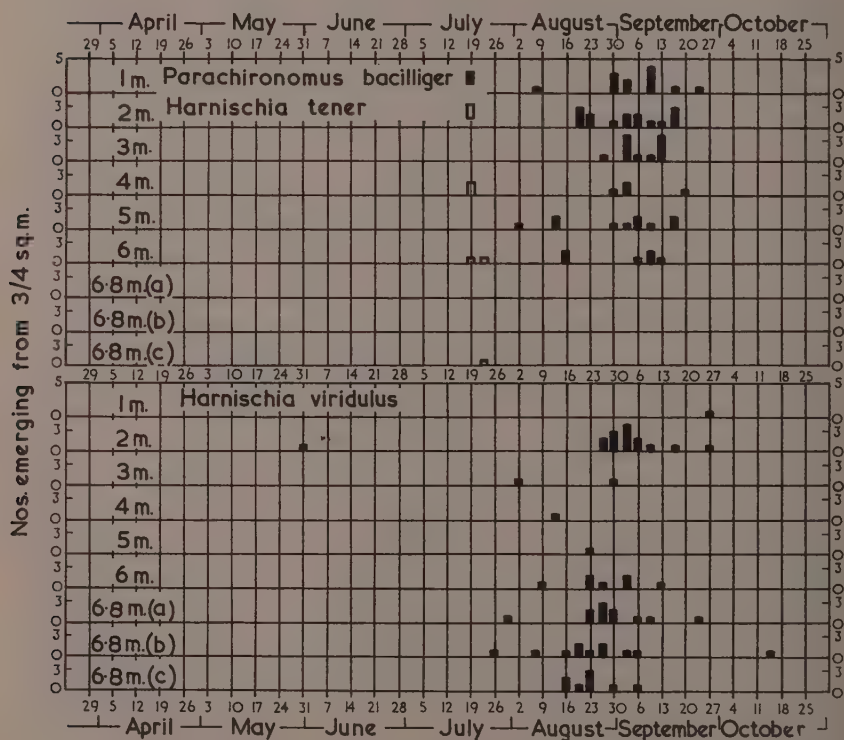


FIG. 21.—The emergences of *Parachironomus vitiosus* from Kempton Park East Reservoir.

FIG. 22.—The emergences of *Parachironomus vitiosus* from Staines South Reservoir.FIG. 23.—The emergences of *Parachironomus bacilliger*, *Harnischia tener* and *H. viridulus* from Kempton Park East Reservoir.

but only one below 6 m. The remarkable concurrence of emergences from 6.8 m. at K.P.E.R. on 23rd July can only be explained by postulating a break in diapause but no such feature is shown by the S.S.R. population. The species is known from oligotrophic and dystrophic lakes (Brundin, 1949).

(16) *Parachironomus bacilliger*.—At S.S.R. 1 male was trapped from 6 m. on 13th September, 1951. The emergences at K.P.E.R. are shown in figure 23. It is not certain whether these are of the first or second generation. Miller (1941) found that *P. tenuicaudatus* Malloch (*P. bacilliger* Kieff.) has one generation at Ontario but at Urbana it probably has two, as it is known to emerge in May (Malloch, 1915: 475). It has been recorded in June in England (Coe, 1950). Lenz (1951) has studied the feeding habits of the larva. It is capable of being a detritus feeder, a predator, a commensal and a parasite; it has been observed living within the gelatinous pupal covering of *Chironomus plumosus*, and feeding on dead *C. plumosus* pupae.

(17) *Harnischia* sp.—A single damaged male caught in trap II 4 at K.P.E.R. on 10th September, 1951, could not be identified. The hypopygium was similar to that illustrated by Thienemann (1951a) for *Cryptocladopelma laccophila* Kieff., but a row of 15 strong setae was present anterior to the anal point.

(18) *Harnischia tener*.—The emergences from K.P.E.R. are shown in figure 23. Four males and 1 female were caught in flight at K.P.E.R. on 12th July, 1951. This species is common in brackish water in Holland (Kruseman, 1933b).

(19) *Harnischia viridulus*.—The emergences from K.P.E.R. are shown in figure 23. At S.S.R. it was not taken below 7 m.; most individuals were caught at 3 m. in the second half of September. In South Sweden this species is common, and the adults can be found from the end of May to the end of August (Brundin, 1949).

(20) *Glyptotendipes paripes*.—At S.S.R. 2 males were trapped, 1 at 3 m. on 23rd August, the other at 4 m. on 20th September, 1951. The emergences from K.P.E.R. are shown in figure 24. There are probably two generations in the year. The ecology of this species has been studied by Wundsch (1943). It occurs in ponds, pools and the littoral of eutrophic lakes and, unlike some other *Glyptotendipes* larvae, it is not a leaf-miner, but feeds on fresh sinking algae. It lives at a depth of 2–3 m. as a rule, where it builds loose formless tubes on empty mollusc shells, especially those of *Dreissena*. Numerous tubes may be built within a single shell.

(21) *Endochironomus albipennis*.—The emergences from K.P.E.R. are shown in figure 25. Here in 1951, 404 males and 363 females were trapped. At S.S.R. the species occurs at all depths. It is bivoltine with a summer optimum of 1 and 2 m. and is a typical inhabitant of the algal mats in eutrophic lakes (Meuche, 1939). The larvae feed on plankton and organic particles, have a filter-feeding mechanism and can build their salivary tubes on the surfaces of leaves of aquatic plants (Walshe, 1951a). They must also, however, be able to live in mud as they occur at depths beyond the range of flowering plants. Their respiration has been studied by Walshe (1951a). They are less able to survive anaerobiosis than *C. tendens* which has more haemoglobin, but are nevertheless capable of filter feeding in water poor in oxygen.

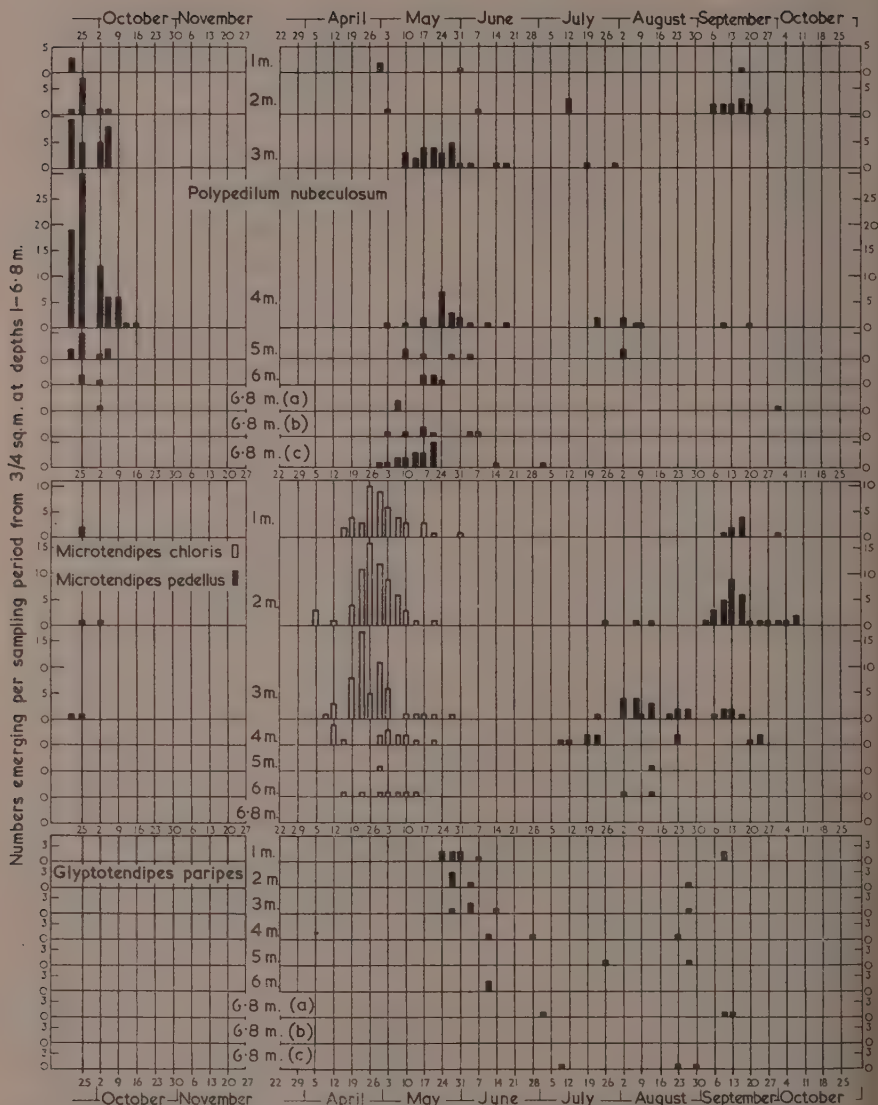


FIG. 24.—The emergences of *Polypedium nubeculosum*, *Microtendipes chloris*, *M. pedellus* and *Glyptotendipes paripes* from Kempton Park East Reservoir.

(22) *Microtendipes chloris*.—At K.P.E.R. in 1951, 88 males and 160 females were trapped. The species is univoltine and emerges in April and May (fig. 24). It occurs most commonly at 1–3 m. and is absent from the profundal. A single male was trapped at 3 m. on 5th April, 1951 at S.S.R. *M. chloris*

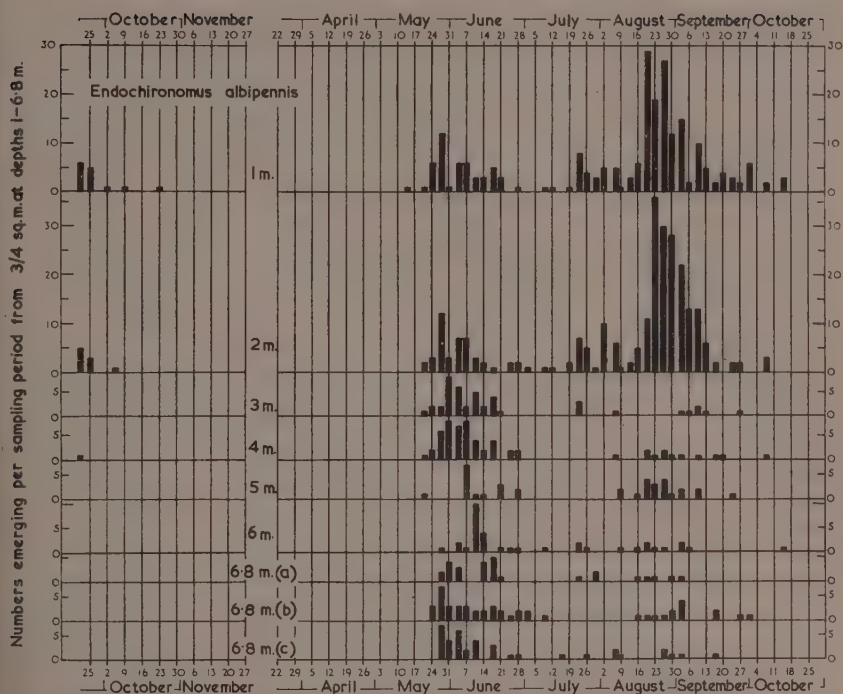


FIG. 25.—The emergences of *Endochironomus albipennis* from Kempton Park East Reservoir.

is a widespread species and occurs both in oligotrophic and eutrophic lakes. The larvae of the genus build short sand or mud tubes and make a special construction for pupation (Lenz, 1941, fig. 60).

(23) *Microtendipes pedellus*.—The emergences are shown in figure 24. In 1951, 48 males and 32 females were trapped. The species was not trapped at S.S.R. It is widely distributed in Europe and occurs in the littoral and sublittoral of eutrophic lakes (Meuche, 1939). The larvae are detritus feeders but do not employ a filter-feeding mechanism (Walshe, 1951b).

(24) *Polypedilum nubeculosum*.—The emergences at K.P.E.R. are shown in figure 24. Here in 1951, 45 males and 61 females were trapped. In 1950 the numbers were 47 males and 83 females. At S.S.R. 1 individual was trapped at 2 m. on 16th July, 1951. Others were caught at 2, 3 and 4 m. on 13th and 30th August, 1951, and on 20th September, 1951. The emergences at K.P.E.R. are interpreted as three generations. The species is widely distributed and common in eutrophic lakes in shallow water. It is much less common in oligotrophic lakes. It may occur in coastal pools. As with *Endochironomus albipennis*, the larva seems capable of being a leaf-miner (Stuart, 1941) and of living in mud-tubes.

(25) *Micropsectra praecox*.—One female, 7th March, 1950, from swarm, Q.M.R.; 1 male, 12th June, 1951 bred from K.P.E.R. mud; 1 male, 7th August, 1951

from swarm, K.P.E.R.; 1 female, 26th November, 1951, from swarm, K.P.E.R. A widely distributed and common species known from rivers, ponds, lakes and brackish waters.

(26) *Tanytarsus lugens*.—Brundin (1947, fig. 99) illustrates the hypopygium of *T. (Calopsectra) borealis* Brund., 1947, which he later decided was synonymous with *lugens* Kieff. (Brundin, 1949:804-5). The reservoir specimens of *T. lugens* fit Brundin's description and figure, but Brundin doubts whether the

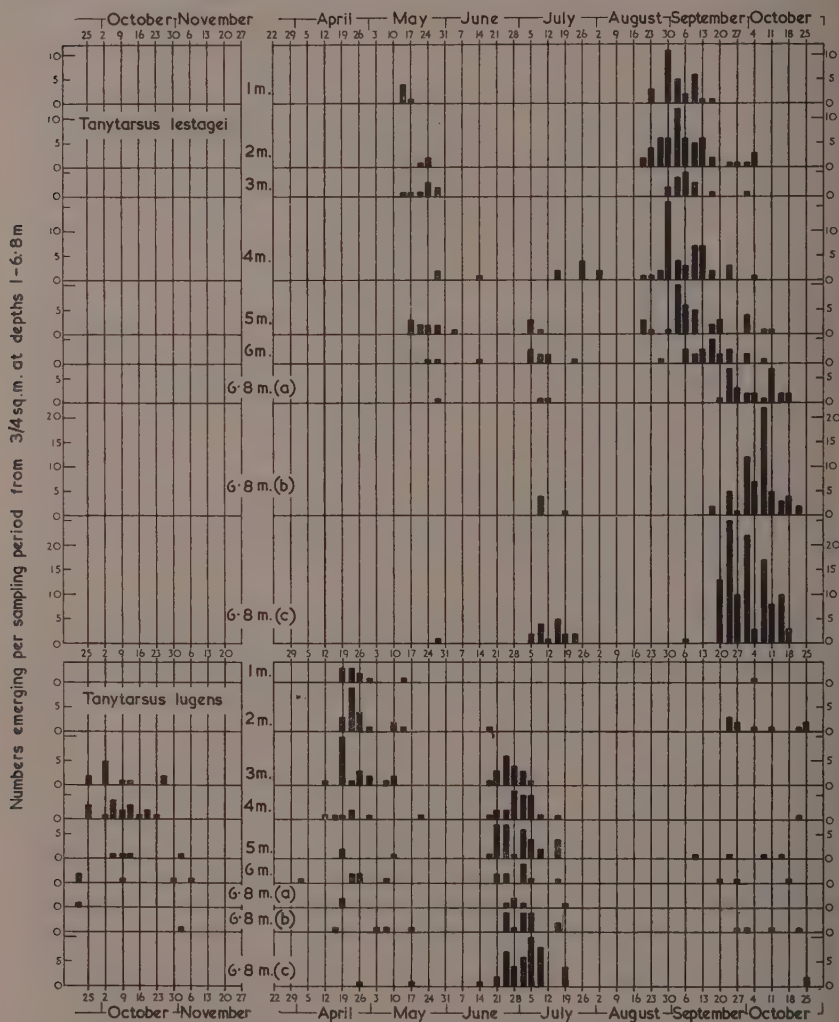


FIG. 26.—The emergences of *Tanytarsus lestagei* and *T. lugens* from Kempton Park East Reservoir.

species Edwards dealt with under this name from the Lea Valley (Edwards, 1929 : 411) is the true *lugens* in view of the great dissimilarity of the habitats of the Swedish and English forms. Brundin also points out that, according to Thienemann (manuscript), the pupa described by Lenz (1927 : 185) from North Sjødalsvand in Norway under the name of *bathophilus* Kieff. is in fact that of *lugens*.

According to Lenz, *bathophilus* has abdominal characters similar to those illustrated by Bause (1913, fig. 61; also Thienemann, 1954, fig. 139b) for *T. bathophilus* Kieff. (syn. *gregarius* Kieff.?), but has a distinctive swim-paddle. The reservoir pupae of *T. lugens*, however, do not fit the descriptions of Bause or Lenz. They correspond more closely with Bause's figure for *T. gregarius* (1913 : 62) but have filamentous hairs confined to segments 7-9. It is possible, therefore, that the English and Swedish *lugens* are separate species distinguishable only in the immature stage.

T. lugens was abundant at S.S.R. and Q.M.R. but less common at K.P.E.R. It was found in very dense swarms in the first week of April at Q.M.R. Observations on its swarming behaviour at S.S.R. are given by Mundie (1956c). The emergences from K.P.E.R. and S.S.R. are shown in figures 26 and 27. They are interpreted as four generations. The first (winter) generation has its mode of emergence at both reservoirs as 26th April for the profundal and 19th April for the littoral. The offspring of this population emerged ten weeks later (about 5th July) in the profundal, thereby having required about 900 day-degrees. The next generation was obliterated in the profundal but is shown in the littoral at 4 m. in S.S.R. with its mode as 9th August (7th August was a five-day sampling period). Assuming that emergences from the profundal occurred one week later than in the littoral, then the modes at S.S.R. would be 5th July and 16th August for the second and third generations. Between these dates about 800 day-degrees had accumulated. From the K.P.E.R. emergences it is found that the winter generation was from 16th October to 26th April, i.e. 190 days and 1125 day-degrees. By applying the formula for thermal summation y is obtained equal to 1.8°C . and K is 770. To check the day-degree requirements of the third generation in the profundal, assuming the mode of its emergence was 16th August, these values can be substituted in the equation

$$(T_3 - y) d_3 = K$$

when d_3 is 42. This gives a value of 840 for $T_3 d_3$. Reference to figure 8 shows that about 750 day-degrees had, in fact, accumulated between 5th July and 16th August in the profundal. The fourth generation has its mode about 11th October in the profundal.

If this interpretation is correct, it follows that *T. lugens* is unable to survive the mid-summer low oxygen concentrations below 7 m. in S.S.R. In K.P.E.R. the small numbers make it uncertain whether it survives at 6-8 m. or not. An important corollary is that the third generation, which is confined to the littoral, has sufficient biotic potential to provide the entire profundal with a dense population of fourth generation larvae.

The validity of these conclusions could only be determined by making estimates of the August population of *T. lugens* larvae in the profundal. This, however, was not done.

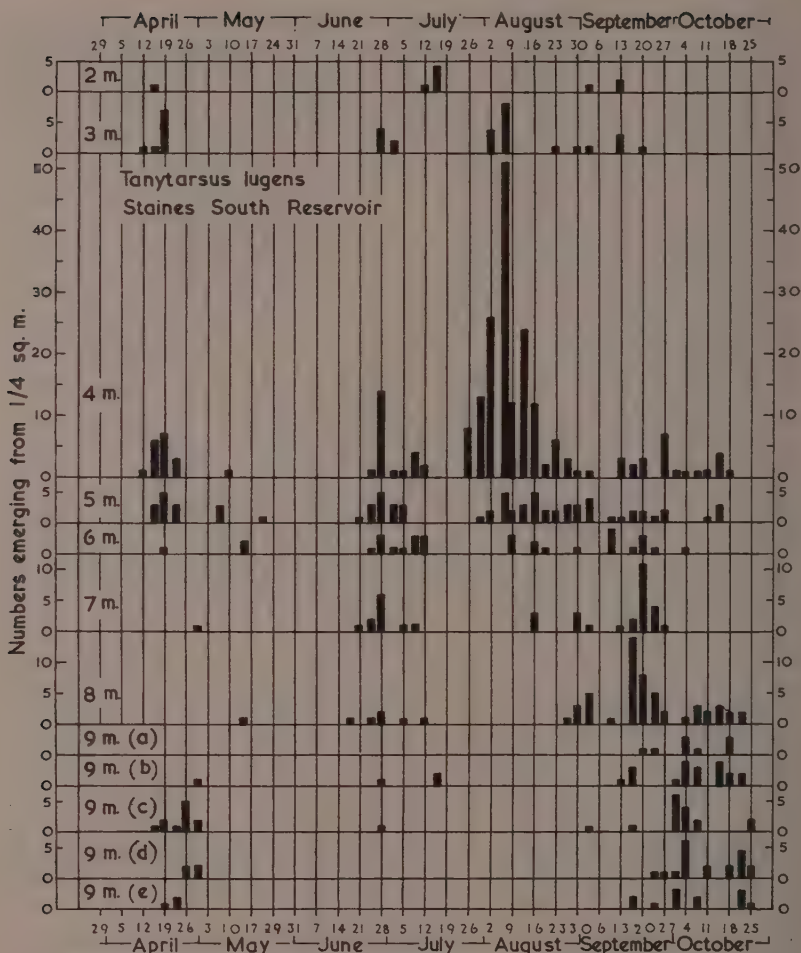


FIG. 27.—The emergences of *Tanytarsus lugens* from Staines South Reservoir.

At K.P.E.R. 95 males and 150 females of *T. lugens* were trapped in 1951.

In South Sweden and middle Europe *T. lugens* is a profundal inhabitant of highly oxygenated lakes and has a narrow (cold) temperature range.

The genus *Tanytarsus* is widely known as the predominant chironomid genus of oligotrophic lakes and it generally occurs in well-aerated water. The finding of *T. lugens* in the profundal of the reservoirs is therefore unexpected. It has evidently adapted itself to low oxygen conditions by virtue of its haemoglobin (cf. Walshe, 1947). That it has not completely succeeded in doing so is shown by its absence from the profundal in midsummer. The members of the genus are algal feeders. The most detailed account of feeding is that of Cavanaugh and Tilden (1930) for *Tanytarsus dissimilis* Joh., which feeds mainly on diatoms. The reservoir species build tubes of mud several times longer than their bodies.

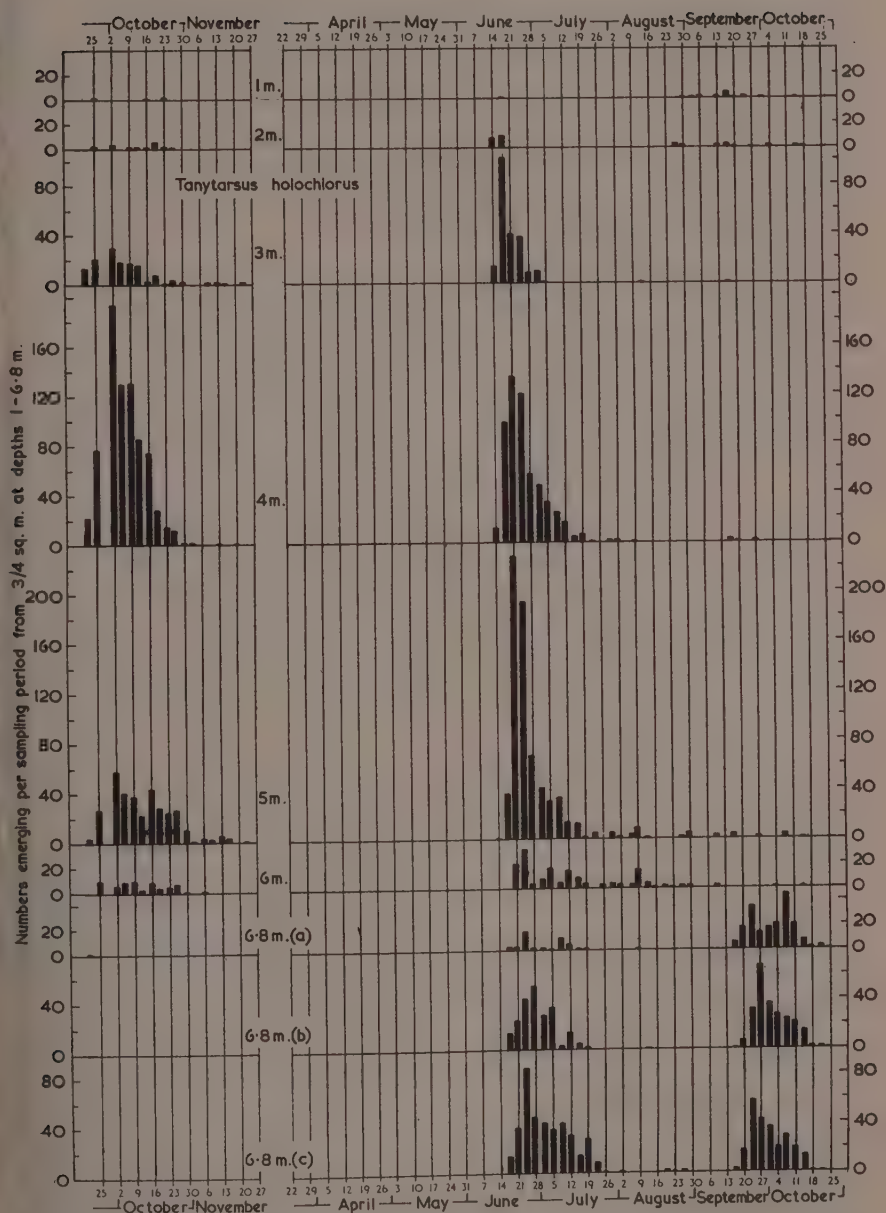


FIG. 28.—The emergences of *Tanytarsus holochlorus* from Kempton Park East Reservoir.

(27) *Tanytarsus lestagei*.—The emergences from K.P.E.R. are shown in figure 26. The second generation was not sufficiently dense in the littoral to have been sampled. It is difficult to explain the time-lag in the autumn profundal emergences. It is not known whether these are of a third or fourth generation. Two hundred and forty-seven males and 238 females were caught. The species was not found at S.S.R.

T. lestagei is one of the most abundant *Tanytarsus* species of the Swedish oligotrophic lakes. It occurs in the subarctic and can become a shallow-water inhabitant of eutrophic lakes (Brundin, 1949). It is recorded from the Grosser Plöner See at 2–3 m. (Humphries, 1938).

(28) *Tanytarsus holochlorus*.—The emergences from K.P.E.R. are shown in figure 28. In 1950, 510 males and 851 females were caught (ratio 1 : 1.66); in 1951 the first generation consisted of 977 males and 1313 females (ratio 1 : 1.34), whilst the second generation consisted of 256 males and 493 females (ratio 1 : 1.92). The numbers caught are given in Table VIII.

The emergences are remarkable in that, in 1951, the numbers emerging from the littoral and sublittoral during September and October were reduced to a few individuals per sq. m., whilst, in 1950, there was a dense population. In the profundal, however, the converse held, there being no emergences from 6.8 m. in October, 1950, whilst in 1951 there was a dense emergence. The reduction of catches from the profundal during the autumn of 1950 is of general application (cf. *P. choreus*, *C. plumosus*, *T. lestagei*) but the features of the littoral emergences are peculiar to *T. holochlorus*. Sufficient numbers were trapped in September 1951 to show that the mode was 17th September, i.e. one week previous to the profundal mode, but no factor, such as water movement or predation, which could be said to have operated in one year but not in the other, can be postulated to explain the almost total obliteration of this littoral population.

The histogram is also remarkable in showing a positive skewness, and a short time-lag of one week between the modes at 3 m. and 6.8 m. suggesting that the species undergoes diapause. Presumably the skewness of the second generation is, therefore, the result of that of the first. The application of the formula for thermal summation, using the day-degree requirements of the overwintering generation in the littoral and the summer generation in the profundal, gives a developmental zero of 2.5° C. Using this estimation, and taking the mode of the second emergence in the littoral as 17th September, the calculated requirements of this generation amount to 1547 day-degrees. From figure 8 it is seen that between 18th June and 17th September in shallow water some 1650 day-degrees had accumulated.

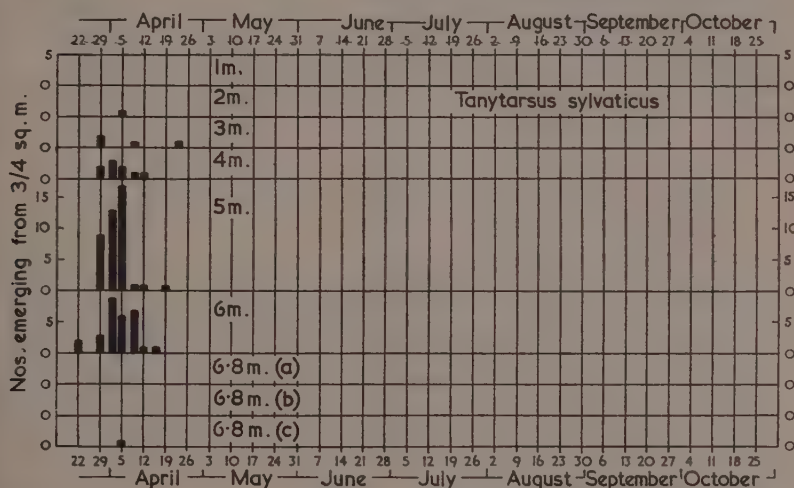
No clear bi-modal distribution was obtained from the catches of *T. holochlorus* at S.S.R. The species was most abundant at 4 and 5 m. and was trapped at 9 m. during September.

T. holochlorus is a widely distributed littoral form (Krüger, 1945). Humphries (1938) records it at 20 m. in the Grosser Plöner See as well as in shallow water.

(29) *Tanytarsus verralli*.—This species was found only in traps at K.P.E.R.; 3 males and 2 females were caught at 2, 3 and 4 m. on 4th and 7th June, and 2nd and 23rd August, 1951.

(30) *Tanytarsus sylvaticus*.—Contrary to Edwards (1929 : 417), the adult male of this species has frontal tubercles, although these are small and may be scarcely visible in pinned specimens. The emergences are shown in figures 13 and 29. This little-known chironomid is univoltine and is one of the first to emerge. It is almost confined to the sublittoral. At K.P.E.R. 46 males and 41 females were caught.

(31) *Cladotanytarsus atridorsum*.—The specimens from K.P.E.R. fall between *Cl. atridorsum* Kieff. and *Cl. difficilis* Brund. (1947). The leg ratio has a range of 1.50–1.77, the mean being 1.62 (20 specimens). On this character the species is *difficilis* but only one male in several hundred had appendage 2a of the



The histogram for *Cl. atridorsum* shows the effects of egg-laying in the profundal by individuals which have emerged from the littoral. The modes of the emergences during June and July at 6 m. are closer together than those of the first and second generations in shallower water. This is not because the species develops more quickly at 6 m. than at 3 m., but is owing to the emergences of the offspring of profundal individuals being swamped by those of the offspring of insects which emerged from the littoral. This is one of the sources of error in the use of the thermal summation formula.

The emergences of the third generation at 6.8 m. are confined to the third week of September and to October. It is possible, therefore, that only those larvae survived which hatched from eggs laid after the overturn at the end of August.

The variation of the total catches of *Cl. atridorsum* is shown in Table VIII. In 1951 the first emergence gave 672 males to 803 females; the second gave 801 males to 913 females; and the third gave 421 males to 624 females.

Cl. atridorsum is common in the littoral zone of eutrophic lakes. It occurs in the Grosser Plöner See.

V. COMMUNITIES, AND INSECTS OTHER THAN CHIRONOMIDS.

One of the first requirements in the study of animal communities is a classification of habitats, and this entails distinguishing those features of the habitats which determine the nature of their communities from those which do not, or are of only temporary significance. A standard classification of benthic habitats does not at present exist. Usually the limnologist merely states some obvious feature such as the presence of *Cladophora* or of numerous mollusc shells, or the absence of oxygen. He always locates the habitat by its depth-zone and treats its community as more or less independent of others without taking into account the possibilities of horizontal exchange of animals between depth-zones (cf. Elton and Miller, 1954: 478).

The general sequence of zones in eutrophic lakes has long been known. Lenz (1923), for example, has illustrated the typical reed-bed, *Potamogeton*, *Chara*, mussel-shell, profundal, sequence. In the reservoirs the zones are homologous except that the reeds are eliminated because of the concrete substratum and a *Cladophora* zone takes their place. Here the Orthocladinae predominate. The *Potamogeton* is sparse and restricted to plants (*P. crispus* L. in Kempton Park East Reservoir) which have gained a foothold between concrete blocks in the littoral. These no doubt support much of the *Cricotopus* fauna which mines in *Potamogeton* (Berg, C. O., 1950). *Chara* is present in K.P.E.R. at a depth of about 4 m. and a mollusc-shell zone (*Dreissena*) also occurs.

In eutrophic lakes the *Tanytarsus* species are mainly confined to the littoral and sublittoral, whilst the profundal is populated by a *Chironomus* and *Procladius* fauna, with perhaps also *Chaoborus* (Culicidae).

In Table IX the species trapped at K.P.E.R. are listed in relation to the depths at which they were caught. It is seen that such a list gives little indication of the differences in composition of the fauna at different depths. To show these a quantitative treatment is necessary both of the winter population and of the changing population throughout the seasons.

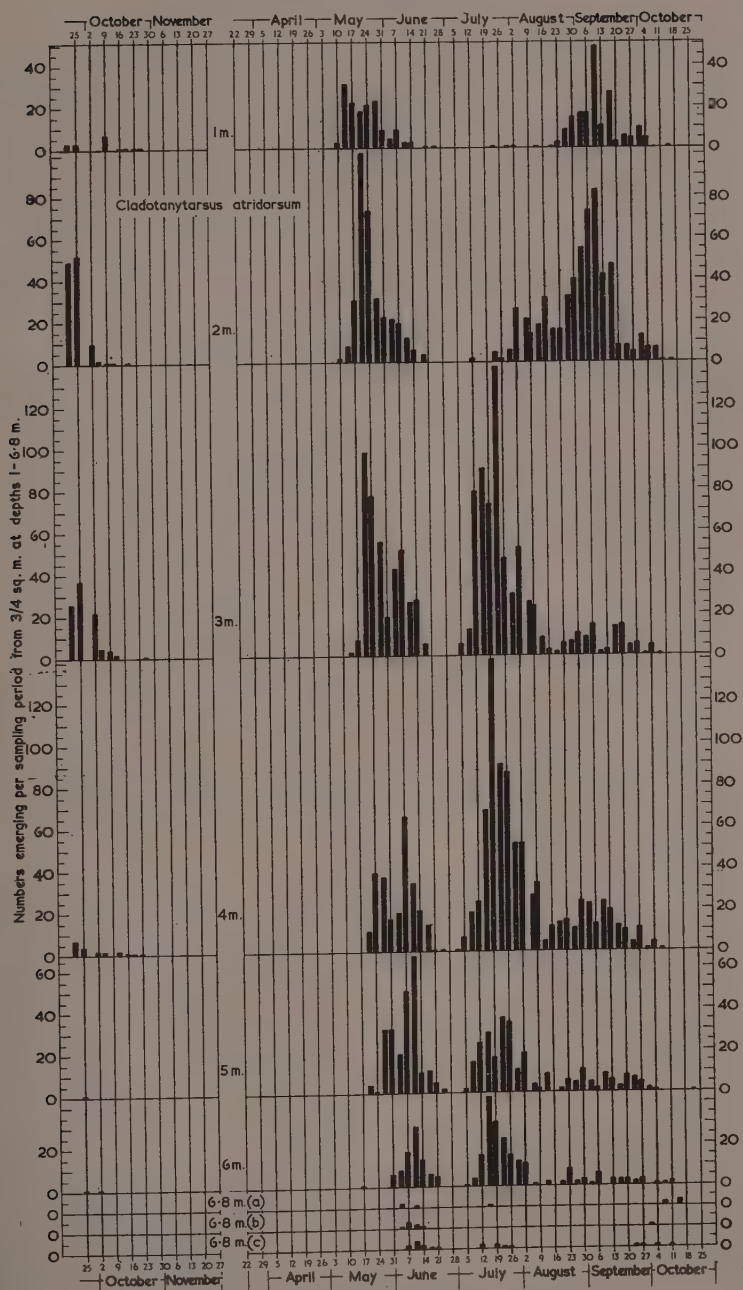


FIG. 30.—The emergences of *Cladotanytarsus atridorsum* from Kempton Park East Reservoir.

The account of the communities at Kempton Park East Reservoir will be confined to a statement of the more obvious features, as many details are deducible from the histograms of emergences. It is based on the total catches of the different species throughout 1951 and is therefore open to criticism, as at different depths the traps do not have the same efficiency, nor are the life-cycles of some species always comparable (e.g. *Tanytarsus lugens*, *T. sylvaticus*). Nevertheless consideration of the total catches brings out the major differences between the zones.

TABLE IX.—Number of trapped species in relation to depth at Kempton Park East Reservoir.

	1 m.	2 m.	3 m.	4 m.	5 m.	6 m.	6-8 m.
<i>Pentaneura monilis</i>	+	+		+	+	+	+
<i>Anatopynia notata</i>	+	+	0	0	0	0	0
<i>Procladius crassinervis</i>	+	+	+	+	+	+	+
<i>P. choreus</i>	+	+	+	+	+	+	+
<i>Psilotanytus rufovittatus</i>	+	+	+	+	+	+	+
<i>Psectrocladius barbimanus</i>	+	+	+	0	0	0	0
<i>P. limbatellus</i>	+	+	+	+	+	0	0
<i>P. stratiotis</i>	+	+	+	+	+	+	+
<i>Cricotopus sylvestris</i>	+	+	+	+	+	+	+
<i>C. dizonias</i>	+	+	+	+	+	0	0
<i>Nanocladius bicolor</i>	+	0	0	0	0	0	0
<i>Lamnoophyes incert</i>	+	0	0	0	0	0	0
<i>Pseudochironomus prasinatus</i>	+	+	+	+	+	0	0
<i>Chironomus cingulatus</i>	0	0	+	+	0	0	0
<i>C. plumosus</i>	0	0	+	+	+	+	+
<i>Lamnochironomus lobiger</i>	+	+	+	+	0	0	0
<i>L. nervosus</i>	+	+	+	+	0	0	+
<i>L. pulsus</i>	+	+	+	+	+	+	+
<i>Cryptochironomus albofasciatus</i>	0	0	0	+	+	+	+
<i>C. biannulatus</i>	0	0	0	+	0	0	0
<i>C. redekei</i>	+	+	+	+	+	+	+
<i>C. vulneratus</i>	0	0	0	+	+	+	0
<i>Parachironomus vitiosus</i>	+	+	+	+	+	+	+
<i>P. bacilliger</i>	+	+	+	+	+	+	0
<i>Harnischa</i> sp.	0	0	0	+	0	0	0
<i>H. tener</i>	0	0	0	+	+	+	+
<i>H. viridulus</i>	+	+	+	+	+	+	+
<i>Glyptotendipes paripes</i>	+	+	+	+	+	+	+
<i>Endochironomus albipennis</i>	+	+	+	+	+	+	+
<i>Microtendipes chloris</i>	+	+	+	+	+	+	0
<i>M. pedellus</i>	+	+	+	+	+	+	0
<i>Polypedilum nubeculosum</i>	+	+	+	+	+	+	+
<i>Tanytarsus lugens</i>	+	+	+	+	+	+	+
<i>T. holochlorus</i>	+	+	+	+	+	+	+
<i>T. lestaei</i>	+	+	+	+	+	+	+
<i>T. verralli</i>	0	+	+	+	0	0	0
<i>T. sylvaticus</i>	0	+	+	+	+	+	+
<i>Cladotanytarsus atridorsum</i>	+	+	+	+	+	+	+
Totals	29	29	30	34	28	25	21
Maximum possible 38.							

Reference to figure 6 shows that the predominant species in all zones, except the sublittoral, are members of the Tanypodinae, *Procladius choreus* (*P. crassi*

nervis) and *Psilotanypus rufovittatus*. The numbers of individuals of Tanypodinae caught per sq. m. at 1, 3, 5 and 6·8 (c) m. in 1951 were 3498, 3622, 1440 and 6011 respectively, while the total numbers of all other species caught per sq. m. at these depths were 2197, 2503, 2044 and 1321. This predominance of Tanypodinae is not, however, shown by the larvae. Analysis of the core samples taken at 6·8 m. on 11th June and 10th September, 1951 showed the percentage composition of the larvae to be approximately 74 per cent. *Tanytarsus*, 21 per cent. Tanypodinae, 2 per cent. *Chironomus plumosus* and 2 per cent. others.

This remarkable discrepancy makes it evident, therefore, that either larval mortality is greatest in *Tanytarsus* or the traps act selectively in favour of the Tanypodinae.

The percentage composition of the larvae in the profundal of Staines South Reservoir in winter was roughly 45 per cent. Tanypodinae, 45 per cent. *Tanytarsus*, and 10 per cent. *Chironomus*. The main qualitative differences from Kempton Park East Reservoir are the presence of *Chironomus anthracinus* and the absence of *Tanytarsus lestagei*.

The percentage composition of the species apart from *Procladius choreus*, *P. crassinervis*, *Pentaneura monilis* and *Psilotanypus rufovittatus* at different depths in Kempton Park East Reservoir is shown in Table X. It is seen from these data that the greatest diversity is found in shallow water, the least in deep (a well known feature of eutrophic lakes), that the Orthocladiinae (least able to resist oxygen deficiency) are confined to the littoral, that *Cladotanytarsus atridorsum* predominates down to 3 m. and *Tanytarsus holochlorus* below 3 m., and that in the profundal *T. holochlorus* is nearly five times more abundant than any other species. Kempton Park East Reservoir is, therefore, a *Tanytarsus* reservoir in accordance with the custom of describing bodies of water in terms of their commonest non-predatory chironomids.

TABLE X.—The percentage composition of species other than Tanypodinae at different depths in Kempton Park East Reservoir based on the annual emergences of the adults.

1 m.		5 m.	
<i>Cladotanytarsus atridorsum</i>	20	<i>Tanytarsus holochlorus</i>	46
<i>Cricotopus dizonias</i>	19	<i>Cladotanytarsus atridorsum</i>	33
<i>Psectrocladius limbatellus</i>	16	<i>Chironomus plumosus</i>	5
<i>Endochironomus albipennis</i>	14	<i>Tanytarsus lestagei</i>	3
<i>Limnochironomus nervosus</i>	9	<i>T. sylvaticus</i>	3
<i>Psectrocladius stratiotis</i>	5	<i>T. lugens</i>	2
<i>Limnochironomus pulsus</i>	4	<i>Endochironomus albipennis</i>	2
<i>Microtendipes chloris</i>	3	15 other species	6
<i>Tanytarsus lestagei</i>	2		
15 other species	8		
3 m.		6·8 m. (c)	
<i>Cladotanytarsus atridorsum</i>	59	<i>Tanytarsus holochlorus</i>	64
<i>Tanytarsus holochlorus</i>	11	<i>T. lestagei</i>	13
<i>Limnochironomus pulsus</i>	8	<i>Chironomus plumosus</i>	7
<i>Microtendipes chloris</i>	4	<i>Tanytarsus lugens</i>	5
<i>Psectrocladius limbatellus</i>	3	<i>Endochironomus albipennis</i>	4
<i>Endochironomus albipennis</i>	2	<i>Cladotanytarsus atridorsum</i>	2
<i>Tanytarsus lugens</i>	2	<i>Polypedilum nubeculosum</i>	2
19 other species	11	9 other species	3

With 57 species, of which 38 were trapped, Kempton Park East Reservoir is poor in species. The proportions of these in the different subfamilies are as follows:

Tanypodinae	. . . 12% (7 species).
Orthocladinae	. . . 35% (20 species).
Chironominae	. . . 52% (Chironomini 40%, 23 species ; Tanytarsini 12%, 7 species).

A detailed comparison could be made of the reservoir findings with what is known of the chironomids of other bodies of water. Thienemann (1954), however, has reviewed at length the chironomid fauna of a great variety of habitats including eutrophic and oligotrophic lakes. It is considered sufficient, therefore, to make only a few remarks.

The factors governing the distribution of chironomids in lakes would seem to be primarily (*cf.* Brundin, 1949; Thienemann, 1954) the history of dispersal of the midges, the water temperature, the oxygen content of the sediments, and the nutritional nature of the substratum. The relation of oxygen to other limnological variables and to total productivity is discussed in the section on productivity (p. 218).

The occurrence of groups of the same or closely related species in similar but widely separated habitats is, of course, one of the most obvious evidences that communities exist. For example Ringsjön in Sweden, which is a natural eutrophic lake (area 40.7 sq. km., max. depth 16.5 m.) has 56 species, of which the following occur in Kempton Park East Reservoir (Brundin, 1949: 461-2):

<i>Pentaneura carnea</i>	<i>Chironomus plumosus</i>
<i>P. monilis</i>	<i>Harnischia viridulus</i>
<i>Procladius choreus</i>	<i>Cryptochironomus vulneratus</i>
<i>Cricotopus sylvestris</i>	<i>Limnochironomus nervosus</i>
<i>Nanocladius bicolor</i>	<i>Microtendipes chloris</i>
<i>Orthocladus semivirens</i>	<i>M. pedellus</i>
<i>Cricotopus bicinctus</i>	<i>Pseudochironomus prasinatus</i>
<i>C. dizoniae</i>	<i>Tanytarsus holochlorus</i>
<i>C. triannulatus</i>	<i>T. lestagei</i>
<i>Chironomus cingulatus</i>	<i>T. verralli</i>

Pentaneura falcigera, *Chironomus anthracinus* and *Cryptochironomus s. str.* (larvae) are also recorded from Ringsjön and species of the genera *Psectrocladius*, *Endochironomus*, *Glyptotendipes*, *Parachironomus*, *Polypedilum* and *Cladotanytarsus* are present.

The reservoir species which are known also in the Grosser Plöner See have already been pointed out. Thienemann (1951c, 1954) has made a detailed comparison of the chironomids of this lake with those of the oligotrophic Swedish lake Innaren and of the Lunzer Untersee. He points out that in such comparisons species lists without quantitative data can be misleading, for the main differences between lakes emerge only when the proportions of species are considered. This applies also to habitats within a lake; for example, a mere list of species gives little indication of the differences between the community at 1 m. and that at 6.8 m. in Kempton Park East Reservoir.

Little information is available to allow a comparison of the fauna of Kempton Park East Reservoir and Staines South Reservoir with that of other reservoirs. Broad similarities, however, can be seen in features of the Ottmachau dam in the Neisse valley in Eastern Germany, as described by Wundsch (1942). These include the presence of an algal habitat with *Cricotopus*, *Glyptotendipes* and *Endochironomus*; of a bare sand and clay habitat with 95 per cent. *Cladotanytarsus* (probably *atr dorsum*), *Cryptochironomus* larvae of the *defectus* group, and *Polypedilum*; and of a deep profundal with *Chironomus plumosus* and *Procladius culiciformis*.

Insects other than Chironomids.

It is convenient to include in this section the observations made on insects other than chironomids. The most notable of these was the culicid *Chaoborus flavicans* Meig.

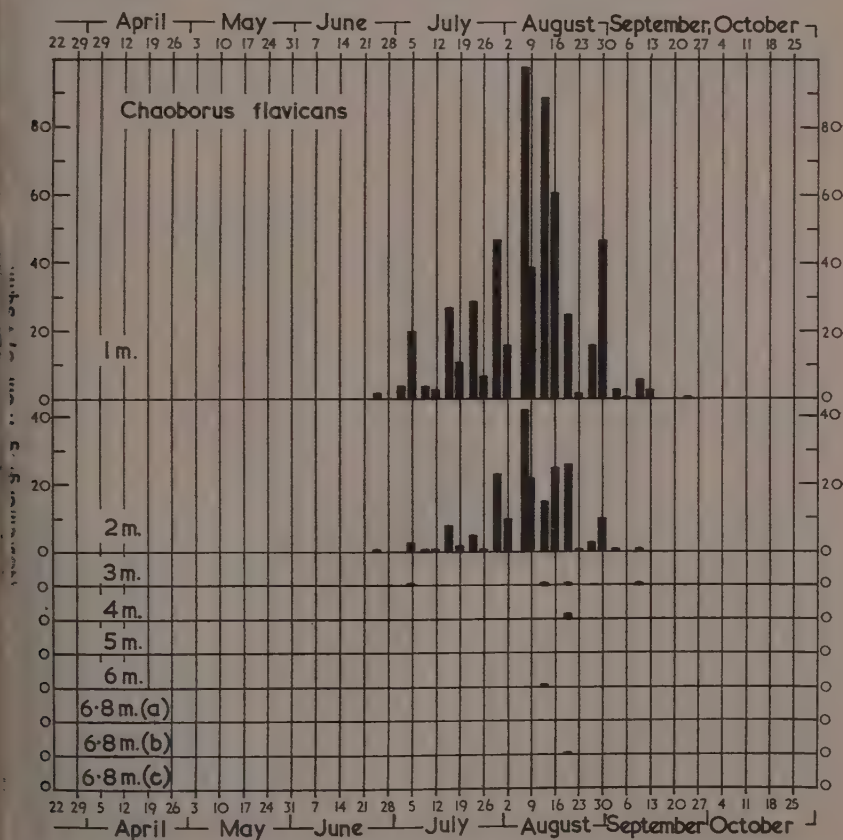


FIG. 31.—The emergences of *Chaoborus flavicans* from Kempton Park East Reservoir.

In June, 1951 the standing crop of *Chaoborus flavicans* larvae at 6.8 m. in Kempton Park East Reservoir was 1033 larvae per sq. m. (based on 12 double-core samples). The subsequent emergences are shown in figure 31. The numbers trapped were 292 males and 476 females. It is clear that there is a migration to shallow water prior to emergence. Borutzky (1939b) found that the larvae and pupae of *Chaoborus* in Lake Beloit migrate from the profundal to the littoral in spring, whilst in autumn a movement in the reverse direction takes place. Scott and Opdyke (1941) and Wood (1953) found similar migrations. The autumn migration can be regarded as a dispersal of the larvae after hatching from eggs laid in shallow water (cf. Berg, K., 1937 : 39-40), although this is not certain. The spring migration remains unexplained. It seems most likely that it is passive, the larvae or pupae remaining near the surface to be carried shorewards by the waves. In April, 1951 the population of *C. flavicans* larvae at 6.8 m. in Kempton Park East Reservoir was 2200 per sq. m. (based on eight single cores) ; in March, 1952 it was 250 per sq. m. (based on 12 double cores) ; in March, April, May and June of 1954 the population was about 40 larvae per sq. m. (based on six single cores per month). Great fluctuations are therefore shown by the population from year to year.

Chaoborus flavicans was not found in Staines South Reservoir nor at Queen Mary Reservoir. The reason for its absence from the larger reservoirs is not known.

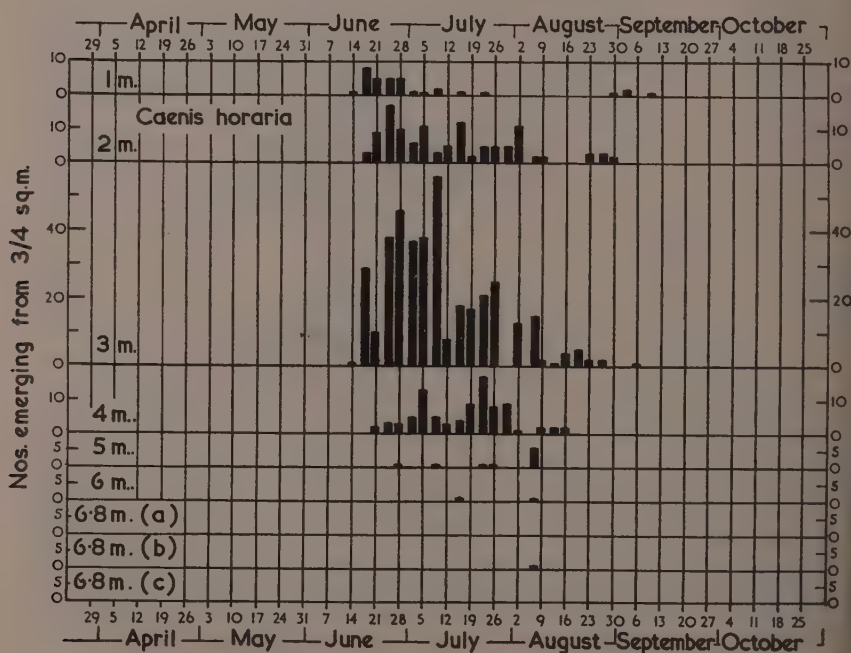


FIG. 32.—The emergences of *Caenis horaria* from Kempton Park East Reservoir.

Caenis horaria L. (Ephemeroptera) was found in great numbers in the littoral of Kempton Park East Reservoir. At 1 m. the population of nymphs during March was over 8000 per sq. m. (plate sample, Mundie 1956b). The emergences are shown in figure 32. The species was found down to 5 m. in Staines South Reservoir.

Caenis moesta Bengtss. was found at Kempton Park East Reservoir. One individual was caught in trap III 3 on 28th June; another in trap II 2 on 16th July.

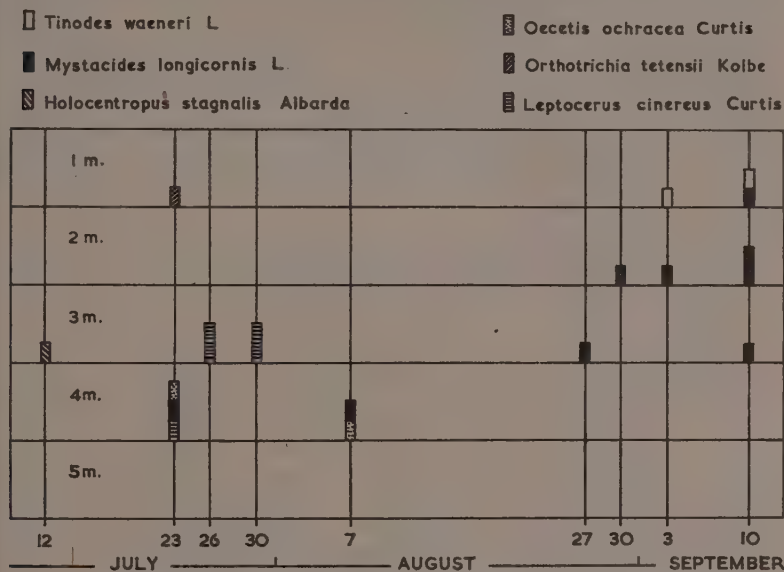


FIG. 33.—The emergences of Trichoptera from Kempton Park East Reservoir.

Each block represents one individual.

Trichoptera were occasionally trapped although most probably emerged from water less than 1 m. in depth. The emergences from Kempton Park East Reservoir are shown in figure 33. Here, in March, the larval population at 1 m. was about 240 per sq. m., but very much higher numbers were present in shallower water.

VI. THE CHIRONOMID FAUNA AS A WHOLE AND THE RELATIONSHIP BETWEEN TRAP AND CORE ESTIMATES.

In an ecological survey of the fauna of an environment it is necessary to distinguish, in practice, two major aspects. One is the distribution of the animals at any one time, the other the changes which take place in this distribution throughout the seasons.

In a lake the fauna is always studied at particular depths so that any general zonation can be described in relation to a definite gradient. It follows that seasonal changes may also be studied at selected points along this gradient.

The strict separation, however, of these two aspects is not possible as the fauna is constantly changing both qualitatively and quantitatively. Nevertheless some point in time must be selected at which the fauna is described so that a basis is provided for continued observations, and it is convenient, though arbitrary, to choose the time when least change is taking place. For temperate lakes, therefore, the close of winter is a suitable date and an estimate made then of the mixed "standing" winter population at different depths can provide a starting point for tracing the changes which occur as the year advances.

In April, 1951 the first Jenkin core samples were taken from Kempton Park East Reservoir at 6.8 m. The counts obtained are shown in figure 34. The mean was 20.2 larvae per core or 5565 per sq. m. (Conversion factor: core count $\times$ 275.5). The following month two further estimations were made. They gave estimates of 8760 and 10,193 larvae per sq. m.

The numbers, therefore, increased almost two-fold between 5th April and 10th May. A *t* test carried out to compare the mean of the April counts with that of the counts on 10th May gives a value of 5.1 for *t*, which, for 18 degrees of freedom, is highly significant.

This increase was wholly unexpected. A decrease in numbers would have been understandable as emergences of *Chironomus plumosus* and *Tanytarsus sylvaticus* were taking place at the time. By 11th June the population amounted to 25,940 larvae per sq. m. (based on 12 double core samples) and this was at the beginning of the major emergences (*Procladius choreus* (fig. 12), *Psilotanyptus rufovitatus* (fig. 14), *Tanytarsus lugens* (fig. 26), *Tanytarsus holochlorus* (fig. 28)).

It is evident that in April and May the main portion of the larval population was not being sampled by the Jenkin sampler. In March and April of the following year, however, quite different counts were obtained. The March numbers were 33,874 per sq. m. and the April ones 42,762 per sq. m., so that an increase again occurred, but at a much higher level. Because no samples were taken in May, 1952, the opportunity was taken to make further estimates in 1954. Counts were then made from six single cores (two cores at each line) taken once a month from February to June. The results obtained are presented in figure 34. It is seen that in 1954 there was a reduction in numbers from February to April from about 36,000 per sq. m. to 12,000 per sq. m., followed by a slight increase in May.

It is clear that great fluctuations take place in the late winter and spring larval numbers. Since these fluctuations are in both positive and negative directions they signify that there is no destruction of larvae, but merely a migration out of reach of the sampler. The larvae are therefore either in the mud below the depth to which the corer reaches or above the corer, in the water itself. In view of the findings obtained by the analysis of larval numbers at different depths in the mud (p. 160) the first possibility is eliminated. To investigate the second, six samples, each of 10 litres of water, were pumped up from close to the mud surface every month in 1954 when the cores were taken, so that counts could be made of any larvae present in the water close to the mud. In these, however, the highest number of larvae found was 12. It would seem, therefore, that the larvae were in the water mass as a whole and not confined to the greater depths.

A number of important questions arises as a result of these findings. Are the larvae, in fact, in the water? If they are (and this would seem to be so)

what causes them to enter it? Do they migrate there on their own account or are they transported there by water movements? If water movements disturb the mud, then the exchange of larvae between it and the water would be expected to occur throughout the winter months when the water is isothermal and winds are strongest. The disturbance, by frictional drag, will be proportional to the square of the wind speed and will occur only when the wind speed has attained a certain value. Table XI shows that an inverse correlation held between the larval numbers and the square of the mean wind velocity of the day previous to sampling in February, March and April, 1954. The data for April, 1951 and March and April, 1952 can be similarly interpreted, but perhaps not those of May, 1951 and certainly not those of November, 1951.

The square of the mean of the previous day's velocities is probably not, however, the most valid statistic to use in investigating a possible correlation between larval numbers and water movement, especially as no allowance is made for changes in wind direction. In spite, therefore, of the above exceptions, the hypothesis that there is a negative correlation seems to offer the most reasonable explanation of the changes in the population.

TABLE XI.—*Standing crop of larvae at 6.8 m. in Kempton Park East Reservoir, and wind velocity at 30 m. above ground.*

Date.	Number of larvae at 6.8 m. in thousands per sq. m.	Square of the mean wind velocity, in km. per hour, of the day previous to sampling.
2.iv.1951	6	259
5.iv.1951		280
3.v.1951		100
10.v.1951	10	75
19.xi.1951	32	208
17.iii.1952	34	36
21.iv.1952	43	54
22.ii.1954	36	16
22.iii.1954	24	115
26.iv.1954	12	129

The increase in numbers of larvae from March to April, 1952 is in part owing to the hatching of the second generation of *Tanytarsus lugens*.

It is evident that, if the above changes are likely to occur in any shallow exposed lake, then estimates of the fauna based on bottom samples obtained during winter may be invalid.

The questions arise: would the reduction occur in much deeper lakes; and what is the maximum depth at which it can take place? Little, however, can be said in answer to these questions. In Staines South Reservoir (maximum depth 9.0 m.) the larval numbers on 10th May, 1951, were 10,000 per sq. m. (based on 12 single cores taken along the trapping line) which are equal to the Kempton Park East Reservoir population on that date, but no estimates for other dates are available to make further comparisons, and the limitations of the Staines South Reservoir trapping data prevent quantitative comparison of the emergences.

In deeper lakes a reduction in animal numbers in spring has been commonly recorded. For example Eggleton (1931) found it (in April) in Third Sister Lake

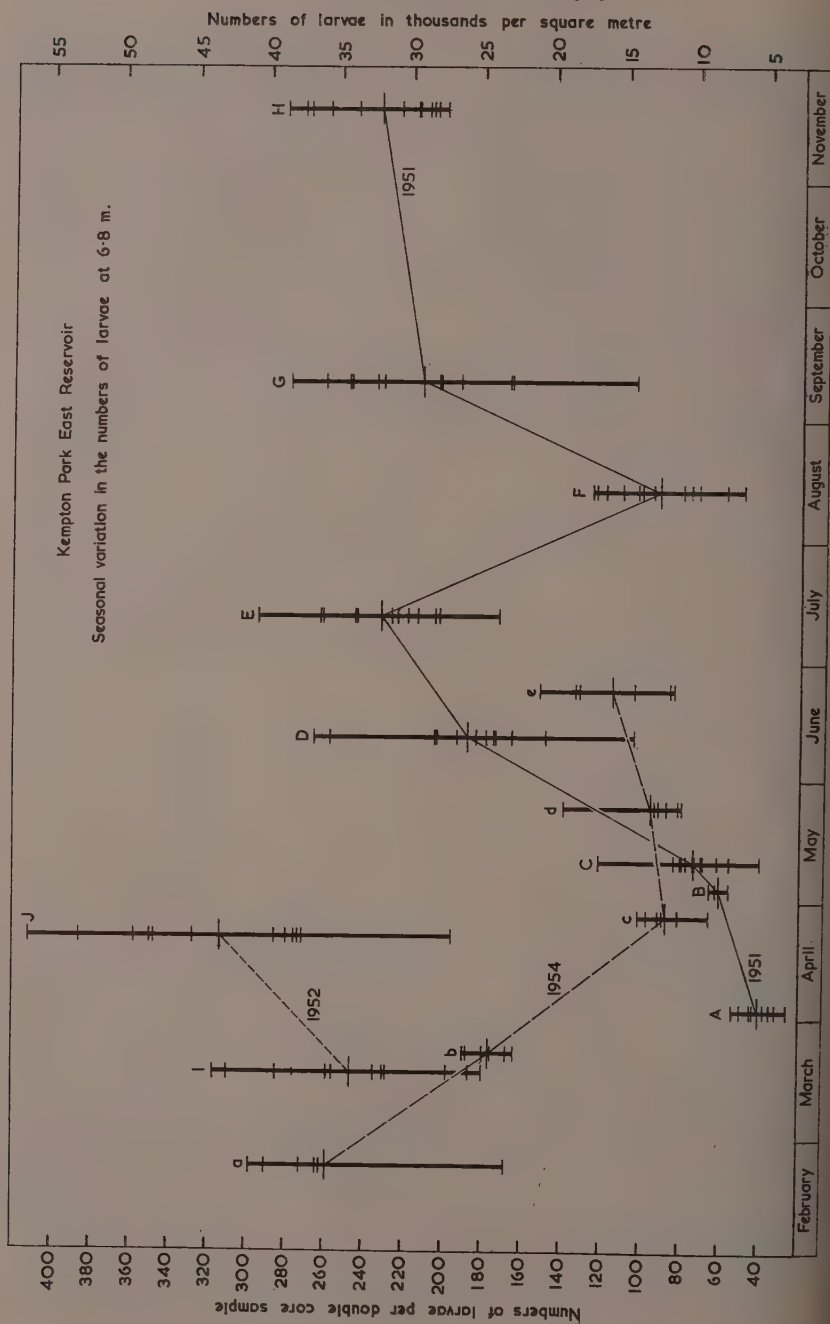


FIG. 34.

below 18 m., and K. Berg (1938) found it in Esrom Lake (22 m.) prior to the main emergences of *Chironomus anthracinus*. In ice-covered lakes a gradual decrease is generally found throughout the winter, followed by a sharp drop in April-May due to emergences following the break-up of the ice (Ball and Hayne, 1952). The reduction below ice-cover is generally considered to be due to predation and mortality resulting from anaerobic conditions (Lindeman, 1942*a*). Low concentrations of oxygen, however, cannot account for Eggleton's observations and almost certainly not for Berg's, as ice-cover was intermittent. It is clear then that the reasons for the reduction are not fully understood and whether any migration of the larvae out of the mud contributes to it is not known.

It is of interest that little numerical change took place in the larval population at 6·8 m. in Kempton Park East Reservoir between November, 1951 and March, 1952.

In summer all the larvae are presumably on the bottom as water movement is negligible (this is evidenced by the slight stratification, p. 219). The summer values for the population at 6·8 m. in Kempton Park East Reservoir are shown in figure 34. As is well known, the numbers of individuals of the temporary fauna (Humphries, 1936) of a lake decrease markedly in midsummer because of departures from the water. This is shown in the August estimates. Part at least of this reduction, however, is only apparent, being the result of the fauna having changed its state rather than its numbers. A great portion of it is now in the form of eggs and early instar larvae which are distributed, as a consequence of the eggs being laid in masses, in widely separated densely concentrated aggregations (*cf.* p. 158). For an estimate of these many more samples are required than are generally taken. They are, of course, lost if coarse screens are used in the washing of the samples (Jónasson, 1955).

The winter population of the littoral and sublittoral zones may now be considered briefly.

The standing population of chironomids on the sides of Kempton Park East Reservoir was sampled by means of a plate sampler (Mundie, 1956*b*). Only one estimate (that for March, 1952) is given (Table XII). Since it is based

FIG. 34.—Estimates of the larval population at 6·8 m. in Kempton Park East Reservoir. The vertical bars represent the ranges, the long horizontal bars the means. These are joined. The short horizontal bars are the core counts and these have been adjusted:

A-H: samples in 1951

in A each short bar represents 1 core count $\times 2$.

in B each short bar represents 4 core counts $\div 2$.

in C each short bar represents 1 core count $\times 2$.

in D-H each short bar represents 2 core counts.

I and J: samples in 1952

in I each short bar represents 2 core counts.

in J each short bar represents 1 core count $\times 2$.

a-e: samples in 1954

in these each short bar represents 1 core count $\times 2$.

on a single series of samples, and because of the method used for subdividing these, the figures must be regarded as approximate (with the exception of the figure for 1.0 m. which is based on a full count). The volumes given exclude stones present on the plates.

TABLE XII.—*Numbers of larvae per sq. m. at different depths in Kempton Park East Reservoir, 13th March, 1952.*

Depth.	Numbers of larvae per sq. m.	Thickness of deposit on plate.	Volume of wet deposit on plate (ml.).
8 cm.	12,000	less than 1 mm.	83
30 cm.	32,000	1 mm.	132
1 m.	46,460	2 mm.	216
1.8 m.	42,000	5 mm.	225
1.8 m.	40,000	5 mm.	206
4.0 m.	16,000	0.5–1.0 cm.	154

If the profundal population for March is taken at about 35,000 larvae per sq. m., then the general distribution of larvae in relation to depth has two maxima, one in the littoral (1–2 m.) and the other in the profundal. This bi-modal distribution is considered characteristic for eutrophic lakes by Lundbeck (1926 : 189, fig. 24, based on weights). In these the numbers usually fall off rapidly below 20 m. (an exception is Lake Simcoe, *see* Rawson, 1930). The low numbers in the sublittoral in the reservoir are no doubt brought about by the nature of the bottom materials which here consist largely of gravel and stones.

The above remarks on the fauna as a whole apply only to the larvae. The emerging fauna can be considered as a whole in terms of numbers of individuals of all species as they emerge from different depths throughout the season. This, however, is not a very meaningful procedure as the curves obtained are the results of independent processes. A more justifiable treatment is to consider the total annual production of trapped insects in terms of weight. This is done in the section on productivity. A certain feature, however, shown by the emerging numbers may be discussed here in relation to the larval population at 6.8 m.

As is seen from figure 36, the total number of insects trapped per sq. m. in traps 7 (50 m. from shore, *cf.* fig. 3) was 2849, whilst in traps 8 (75 m. from shore) there were 6520 and in traps 9 (125 m. from shore) there were 7338. It would be expected from these figures that the larval population at 6.8 m. would show a similar reduction in numbers near the shore. The simplest way to test this is to examine the totals of all the core counts taken throughout 1951 at different distances from the shore. At about 25, 60, 90, and 125 m. from the west shore these amounted respectively to 3254, 2959, 3048 and 2912 larvae and therefore show no significant differences. The low catches obtained 50 m. from the shore are probably mainly due to faulty sampling, particularly at trap II 7.

Table XIII gives the total numbers of midges caught in each trap during 1950 and 1951 at Kempton Park East Reservoir. The single trap 10 used in 1950 has been omitted. The data show the variation in catches from the same depth. For the most part the extents to which this variation is the result of technical faults in sampling and to real variation in the population are unknown.

TABLE XIII.—Total numbers of chironomids caught per trap at Kempton Park East Reservoir during September–November, 1950 and March–October, 1951.

September–November, 1950.			
Trap.	Line I.	Line II.	Line III.
1 .	354	760	373
2 .	147	211	270
3 .	248	211	162
4 .	290	417	370
5 .	129	171	140
6 .	24	53	64
7 .	1	17	12
8 .	0	10	6
9 .	0	0	3
Total .	1193	1850	1400

March–October, 1951.			
Trap.	Line I.	Line II.	Line III.
1 .	1712	1703	852
2 .	1343	2753	1020
3 .	973	1465	2125
4 .	1005	1021	1994
5 .	493	1272	838
6 .	484	969	317
7 .	1494	189	454
8 .	2326	608	1956
9 .	1975	1533	1996
Total .	11,805	11,513	11,552

The Relationships between the Numbers of Benthic Larvae and the Numbers of Trapped Chironomids.

The following approximate calculations show the discrepancy between the estimated benthic and emerging populations.

If the June core samples are taken as valid, *i.e.* if all the larvae were then in the mud, they give an estimate of the fauna prior to the main emergences, although some species (*e.g.* *Tanytarsus sylvaticus*, *T. lugens*) have emerged by this month. Figure 34 shows the numbers of larvae obtained on 11th June from 12 double core samples at 6·8 m. in Kempton Park East Reservoir. These counts give an estimate of 26,000 larvae per sq. m. and the subsequent emergences are given in Table XIV. Here, and in the following calculations, the estimate of emergences from 6·8 m. is based on catches in traps 8 and 9. Catches in trap 7 have not been used because of faulty sampling. Sampling error can be assumed to be always in one direction, *i.e.* to give too low a count, and the higher figures for traps 8 and 9 are taken as nearer the true numbers of emerging insects.

The total number of insects caught in six traps was 9016 or 6012 per sq. m. Therefore 23 per cent. of the benthic population was subsequently trapped.

This estimate, however, is open to criticism. The emergence period of the two commonest species lasted nine and ten weeks respectively, and some mortality of the larvae would occur throughout these times. Similarly, mortality

TABLE XIV.—The emergences of the first generation of chironomids after 11th June from 6.8 m. at Kempton Park East Reservoir.

Species.	Sampling period.	Traps 8.	Traps 9.
<i>Procladius choreus</i> . . .	12 June–16 Aug.	1486	1737
<i>P. crassinervis</i> . . .	12 June–16 Aug.	103	117
<i>Psilotanypus rufovittatus</i> . . .	12 June–23 Aug.	1354	1825
<i>Chironomus plumosus</i> . . .	12 June–25 Oct.	115	46
<i>Cryptochironomus vitiosus</i> . . .	25 June–29 July	16	14
<i>Endochironomus albipennis</i> . . .	11 June–2 July	13	7
<i>Tanytarsus lugens</i> . . .	14 June–19 July	15	42
<i>T. holochlorus</i> . . .	18 June–2 Aug.	216	386
<i>T. lestagei</i> . . .	5 July–23 July	5	16
<i>Cladotanytarsus atridorsum</i> . . .	12 June–21 June	7	10
Total		9016	

must have occurred in the development of the second generation of *Chironomus plumosus*. As against these losses, however, there were over 800 egg masses (mainly of *Tanytarsus lugens* and *lestagei*) per sq. m. in the profundal on 11th June and the larvae produced from these are not included in the estimate.

It is of interest to compare the catches obtained in the profundal with those in the littoral. For this purpose an estimate of the total numbers of larvae at 1.0 m. may be used. On 13th March, 1952, the number of larvae at 1.0 m. was 46,500 per sq. m. The first emergences in 1951 amounted to 3268 per sq. m., which is 7 per cent. of the benthic population of 1952. Assuming, therefore, that the littoral population in 1951 was of about the same density as in 1952, mortality at 1 m. is three times that in the profundal. That mortality is higher in the littoral is certain (Ball, 1948; Ball & Hayne, 1952) but part of this difference is perhaps owing to the greater ability of the insects to avoid traps in shallow water.

No data, unfortunately, are available on the size of the fish population of Kempton Park East Reservoir.

A more satisfactory calculation can be made from the three species of Tanypodinae in the profundal, *Procladius choreus*, *P. crassinervis* and *Psilotanypus rufovittatus*, taken together. These, being predators, can be assumed to have a lower mortality in their late instars than the *Tanytarsus* species. The numbers of tanypodiniid larvae found on 11th June at 6.8 m. gave a mean of 5565 per sq. m. The subsequent emergences of these species (Table XIV) amounted to 4416 per sq. m. or 79 per cent. of the larval population. Borutzky (1939b), working on Lake Beloie (maximum depth 13 m.), obtained catches of *Tanypus* equal to 76 per cent. and 55 per cent. of the larval population.

A similar calculation based on the second emergence of the Tanypodinae cannot be made without distinguishing the larvae of *P. choreus* from *Ps. rufovittatus*, as the latter has only one generation per year in the profundal.

On 11th June the mean number of individuals of large (third and fourth instar) *Tanytarsus* larvae was 7989 per sq. m. The emergence in June and July of *T. holochlorus*, *T. lestagei* and *T. lugens* amounted to 452 per sq. m. or 5.6 per cent. of the larval population. It appears, therefore, that a high mortality occurs among the *Tanytarsus* larvae, or that the pupae, which are more delicate than those of the Tanypodinae, perish readily on the sides of the traps before

reaching the jar. A similar very low percentage is shown by the September and October emergences. On 10th September the mean number of *Tanytarsus* larvae of all sizes at 6·8 m. in Kempton Park East Reservoir was 22,260 per sq. m. The subsequent emergences (figs. 26 and 28) amounted to 444 per sq. m. or 1·9 per cent. of the larval population.

On 10th May the mean number of fourth instar larvae of *C. plumosus* at 6·8 m. in Kempton Park East Reservoir was 939 per sq. m. On 11th June the number was 757 per sq. m., the difference between the two populations therefore being 182. From 11th May to 11th June the number of individuals of *C. plumosus* which emerged in traps 7, 8 and 9 amounted to very nearly 16 per sq. m., or 8 per cent. of the above difference.

If *C. plumosus* emerges randomly, a total of 36 individuals for 9 traps has 95 per cent. confidence limits of 25·1 and 49·8. Consequently the limits of the catch as a percentage of the larval population are 6 per cent. and 11 per cent. Limits of error could also be used for the core samples and taken into account in the estimate of the trap's efficiency, but the uncertainties inherent in trapping make such calculations unjustifiable.

On 3rd May the mean number of *C. plumosus* larvae was 1405 per sq. m. The difference between this population and that of 10th May is 466 per sq. m. During this week about four adults emerged per sq. m., i.e. less than 1 per cent. of this difference. On 13th August the larval population amounted to 675 per sq. m. On 10th September it was 103 per sq. m. The difference between the two estimates is therefore 572. From 14th August until 10th September the mean number of *C. plumosus* trapped at 6·8 m. (traps 7, 8 and 9) was 88 per sq. m. or 15 per cent. of this difference. The remainder of this emergence gave a similar catch. Thus 15 individuals were trapped per sq. m. after 10th September, i.e. 14 per cent. of the larval population on 10th September.

Borutzky (1939a) obtained catches of *C. plumosus* equal to 17 per cent. and 13 per cent. of larval populations prior to emergence. It is of interest that he found the difference between catches in traps set near the bottom and those in traps set below the surface to amount to only 4 per cent.

A trapping efficiency of 2 per cent. was found for *Polypedilum nubeculosum* with a larval population of 762 per sq. m.

On 13th August nine double-core samples taken at 6·8 m. from Kempton Park East Reservoir were examined for *Endochironomus* larvae. None was found. Nevertheless from 16th August to 6th September a mean of 9·7 individuals of *E. albipennis* was trapped per sq. m. at 6·8 m. The upper 95 per cent. confidence limit for a total of 0 is 3·7. For nine double cores this gives 55 larvae per sq. m. and therefore the maximum possible trapping efficiency is 17 per cent.

The finding of no larvae of *Endochironomus* on 13th August, however, raises the question whether all the *Endochironomus* population was in the mud or not. If exchanges of larvae between the mud and water can occur after the onset of thermal stratification, as well as before, then estimates of trapping efficiency are rendered even more uncertain.

In conclusion it may be said that, since natural mortality occurs in the benthic population and among the ascending pupae (Borutzky, 1939a, b), the trap is not as inefficient as is indicated by the above catches. It seems certain, however, that it is not 100 per cent. efficient, even when set near the mud at 6·8 m. It is possible (Mundie, 1956a) that the avoidance of the traps by the

insects occurs mainly when they come into contact with the sides of the trap very near the base, and that if they ascend near the centre of the mouth of the cone they continue their ascent. If this is so, the greater the area of the trap in relation to the perimeter of the mouth the more efficient the trap will be. Thus large traps should be more efficient than small ones, although beyond a certain size other factors may operate to affect efficiency.

VII. PRODUCTIVITY.

Biological productivity, or the rate of production of organic matter, may be regarded as the central issue in limnology and the one which unifies diverse researches. Lake productivity studies can be concerned with the estimation of the total amount of organic material produced in a lake, or in a unit of it, in a given time, or they can deal with only one form which the organic matter can take, e.g. dissolved organic matter, phytoplankton, bottom flora, zooplankton, bottom fauna, or fish. As is well known these different levels of organisation constitute, in general terms, a nutritional series of which the members have complex interrelationships. Productivity studies, in the widest sense, are as much concerned with the elucidation of these as with the assessment of final products (Lindeman, 1941 ; Mare, 1942).

It follows, therefore, that if the production of only one group of organisms (such as the Chironomidae) is studied, conclusions which might be drawn are immediately limited by lack of information on other groups. It is therefore possible to discuss the productivity of the reservoir chironomids in general terms only.

The subject has two distinct aspects. One is the rather special question of the relationship between the *kinds* of chironomids living in the reservoirs and the total productivity of the reservoirs ; the other is the more general one of why the reservoirs are highly productive of chironomids.

Much has been written on the relationship between the level of productivity of a lake and the kind (group, genus or species) of chironomid which predominates in its profundal (see literature cited by Brundin (1949) and Thienemann (1954)). Here the subject will be only briefly reviewed in order to state its present position, and to show the bearing on it of the survey's findings.

The classification of lakes into oligo-, meso-, and eutrophic types, based (Naumann, 1919) on the supply of nutrient (edaphic or geochemical) materials to the lake, and on the primary or photosynthetic productivity resulting from this, is widely adopted today although the terms have no generally accepted precise quantitative limits. Ever since the early work of Thienemann (1923) and Lenz (1925) attempts have been made to associate different kinds of chironomids with these levels of productivity and some success has been achieved. Thus both continental and American workers (e.g. Lenz, Brundin, Deevey) have shown that genera of the Orthocladinae are found predominating in the profundals of extremely oligotrophic lakes, the genus *Tanytarsus* occurs in less extreme oligotrophic lakes, several genera of Chironomini without ventral tubules occur in mesotrophic lakes and members of the genus *Chironomus sensu stricto* with ventral tubules live in eutrophic lakes. Moreover, Deevey (1942) has shown that within the stratified postglacial sediments of a single lake the fossil chironomids show a succession from *Tanytarsus* through *Endo-*

chironomus to *Chironomus*, correlated with the lake's evolutionary sequence from oligotrophy to eutrophy.

It would seem, therefore, that the kind of chironomid living in the profundal of a lake may be taken as a good indicator of the level of the lake's productivity.

The occurrence, however, of exceptions to this generalisation (e.g. Miyadi's (1933) oligotrophic *Chironomus* lake), and a fuller understanding of the factors governing productivity are making it apparent that the association of chironomid type and lake type is not direct, but is bound up with the supply of oxygen to the sediments. This in turn is related to the factors of nutrient materials and lake morphometry.

The relationships of productivity, oxygen content of the hypolimnion and lake morphometry have been discussed by Hutchinson (1938) and Mortimer (1942) among others. They may be described in the most general terms as follows: In summer when rising temperatures bring about a density stratification of the water, the thermocline which develops seals off the hypolimnion from access to atmospheric and photosynthetic oxygen, and all organic matter sinking from the epilimnion therefore uses up, for its oxidation, hypolimnetic oxygen. The removal of this oxygen takes place primarily at the mud surface and it is because of this that the bottom fauna is affected. As summer advances the amount of oxygen used up will depend on the amount of organic matter to be oxidised and upon the amount of oxygen available. The last will depend in turn upon the mean depth of the hypolimnion. From a very deep hypolimnion only a small percentage of the available oxygen may be used in decomposition; from a shallow one all may be used and anaerobic conditions be established.

A shallow oligotrophic lake, therefore, though poor in nutrient materials may develop a high oxygen concentration deficit due to the morphometric factor. In contrast, a lake rich in nutrients derived from the surrounding watershed, and hence highly productive of phytoplankton, might have so large a hypolimnion that there would be little utilisation of hypolimnetic oxygen. This, however, is somewhat hypothetical. There are no highly productive very deep lakes, probably because deep lakes tend to lie in unfertile watersheds.

The relation, then, between oxygen deficit and primary productivity is not necessarily simply inverse. Moreover two further factors complicate it. One is the ratio of the loss of organic matter through the outflow of the lake to its gain from inflowing waters; the other is the amount of gaseous exchange between the epi- and hypolimnion due to diffusion. In the above account both are neglected.

The relationship is therefore complex, but it is clear that it is the oxygen deficiency and not the productivity which determines the kind of chironomid which predominates in the profundal. It so happens, however, that in very many lakes eutrophy is associated with a high oxygen concentration deficit, and oligotrophy with a low deficit, so that a correlation between lake type and chironomid type emerges.

In Kempton Park East Reservoir, although it is strongly eutrophic, complete absence of oxygen did not occur in midsummer in 1950 or 1951 (fig. 35). This is the result of the slight and intermittent stratification of the water. The reservoirs are usually insufficiently deep to develop a marked thermocline and in 1951 at Kempton Park East Reservoir the maximum difference in temperature between surface and bottom waters was only 2.5° C. In highly eutrophic

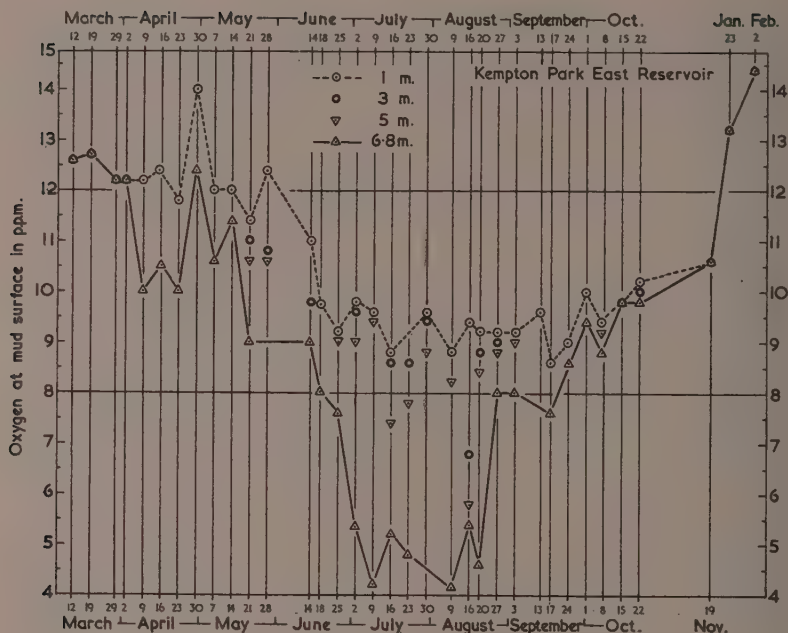


FIG. 35.—For explanation see text.

waters this is sufficient to bring about oxygen depletion at the bottom with its attendant chemical changes. Complete absence of oxygen may occur in very hot summers.

The summer oxygen content of the water close to the mud in Kempton Park East Reservoir is low, but is not zero. Consequently the profundal is populated by a varied chironomid fauna consisting of *Tanytarsus*, *Endochironomus* and *Chironomus* with littoral elements *Microtendipes*, *Polypedium* and *Limnochironomus*. The Tanypodinae being free-living predators and less intimately dependent on benthic conditions than the phytophagous and detritus-eating forms are not regarded as having any great indicator value.

No determinations were made of the midsummer oxygen conditions in Staines South Reservoir. It is certain, however, that the greater depth, by imposing a greater stability on stratification, results in a lower oxygen content than at Kempton Park East Reservoir. Consequently the profundal fauna is a *Chironomus plumosus*, *C. anthracinus* one with the anomalous *T. lugens* abounding most of the year but not surviving the adverse midsummer period.

It may finally be pointed out that the chironomid series found in a series of lakes of increasing oxygen deficiency in midsummer can also be found down the depth-zones of a single lake, as is shown by the reservoir findings where the sequence at optimum depths, commencing from shallow water, is Orthocladiinae, *Tanytarsus*, *Endochironomus* and *Chironomus*. To attribute the series within different lakes to the single factor of oxygen is no more satisfactory

than it is to attribute the zonation in the reservoirs to oxygen alone. All explanations of animal distributions in terms of a single factor are easily overstressed.

Much of the literature on the standing crops of chironomids in lakes in different parts of the world has been reviewed by Thienemann (1954 : 680-726). The data show that the number of chironomid larvae is much lower in the profundals of oligotrophic lakes than in eutrophic lakes ; that it is usually much higher in littorals than in profundals ; but that it may not be very different in the littorals of the two lake types.

The size of standing crop will be determined either by the size or by the rate of production of its food supply (Clarke, 1947). Thus benthic productivity is mainly dependent on trophic factors, except on the rare occasions (in lakes) when climatic factors destroy standing populations. An example of this is the destruction of mayflies in Lake Erie caused by exceptionally low oxygen concentrations (Britt, 1955).

The dependence, directly or indirectly, of the benthos on primary (photo-synthetic) productivity is shown by a comparison of primitive and evolved lakes, the differences between which are mainly the result of differences in rates of erosion of the drainage areas (Pearsall, 1921). These determine not only the physical characters of a lake but also the nutrient content of the water. This content is greatly increased, and hence production accelerated, by agricultural practice in the surrounding land, but this itself is possible only as a result of processes of weathering and erosion.

It is the geochemical or edaphic factor, therefore, which determines the hyperbolic relationship between mean weight of bottom fauna and mean depth of lake (Rawson, 1955). That this is so is made plain by the fact that " no fundamentally oligotrophic lakes yet known are so shallow as to be morphometrically eutrophic " (Deevey, 1941 : 450) and that where a deep lake is found to be exceptionally productive it is influenced by urban or agricultural drainage (Hasler, 1947).

The reservoirs dealt with here are eutrophic. Obvious features associated with their high production are the alkaline nature of the water, the high bicarbonate hardness, and the rich silicate, phosphate and nitrogen contents derived from sewage and industrial discharges into rivers (Taylor, 1955). Data on the chemistry of the Thames water before entering the reservoirs are given in Table XV.

TABLE XV.—*Chemical averages for 1951 expressed in p.p.m. for River Thames water at Walton.*

(From the Thirty-fifth Report of the Metropolitan Water Board).

Ammoniacal nitrogen	0.267	Total hardness	Phosphate as PO_4
		258	0.39
Albuminoid nitrogen	0.226	Permanent hardness	Silica as SiO_2
		81	14
Oxidised nitrogen	4.3	pH value	B.O.D.
		7.9	2.3

A few observations were made on the chemistry of the mud at Kempton Park East Reservoir. The loss on ignition was 36.94 per cent. (June sample at 6.8 m.) ; its calcium carbonate content was probably 55-60 per cent. of the

dry weight, a figure cited for the mud of a nearby reservoir (Mackenzie, 1938 : 46); its organic carbon content (Walkley and Black values, Piper, 1944 : 224) was found to have an annual mean of 5.63 per cent. at 1 m. and 3.92 per cent. at 6.8 m.; the highest values (6.59 per cent. at 1 m., 4.16 per cent. at 6.8 m.) being found in May.

While correlations between benthic production and other measured limnological variables, either chemical or biological, may be suggestive of causal relationships, an understanding of the mechanism of production of the benthos can be reached only by the analysis of its food relations. What this involves has been discussed by Lindeman (1942c) for a lake, and, in greater detail, by Mare (1942) for a marine area. The contribution of a survey to this analysis is slight, and is confined to assessments of the quantities of organisms taking part at particular times in the energy exchanges. The following data are presented from Kempton Park East Reservoir.

Table XVI gives estimates of the weight of the standing crop of larvae at 6.8 m. in different months. Dry weights were obtained on heating alcohol-preserved material for 15 hours at 110° C.

TABLE XVI.—*Estimates of the standing crop of chironomid larvae at 6.8 m. in different months at Kempton Park East Reservoir.*

Date.	Sample.	Number of larvae.	Dry weight in gm.	Dry weight in gm./sq. m.
12.vii.51	II 4, 2 cores	234	0.0290	3.993
19.xi.51	I 1, 2 cores	246	0.0322	4.433
17.iii.52	I 2, 2 cores	273	0.0454	6.251
17.iii.52	II 4, 2 cores	262	0.0308	4.241
22.ii.54	I 4, 1 core	131	0.0099	2.727

If a mean weight of 5.25 gm. per sq. m. is taken as the late winter biomass, this gives a dry weight of 52 kilograms per hectare or 46.2 lb. per acre. Taking 85 per cent. as the water content of the larvae (Juday, 1922 ; literature cited by Thienemann, 1954 : 657) the mean wet weight for March is 346 kg. per hectare. This is comparable to the mean weights of total bottom fauna for Lake Mendota (414 kg./ha, Juday, 1942) and Linsley Pond (348 kg./ha, Deevey, 1941).

TABLE XVII.—*Mean weight in mg. of one adult male and one adult female of different species.*

<i>Psilotanytus rufovittatus</i> . . .	0.2052	<i>Endochironomus albipennis</i> . . .	0.7820
<i>Procladius choreus</i> —male . . .	0.4110	<i>Pseudochironomus prasinatus</i> . . .	0.4068
female . . .	0.5622	<i>Microtendipes chloris</i> . . .	0.7259
<i>Pentaneura monilis</i> . . .	0.2251	<i>Polypedilum nubeculosum</i> . . .	0.3325
<i>Psectrocladius limbatellus</i> . . .	0.1938	<i>Tanytarsus lugens</i> . . .	0.1899
<i>Cricotopus dizoonias</i> . . .	0.0642	<i>T. holochlorus</i> . . .	0.1503
<i>Chironomus plumosus</i> . . .	3.6033	<i>T. sylvaticus</i> . . .	0.3281
<i>Limnochironomus pulsus</i> . . .	0.3232	<i>Cladotanytarsus atridorsum</i> . . .	0.0692

The total weight of chironomids trapped at Kempton Park East Reservoir was calculated from the data in Table XVII. Weights for species not listed were read from a curve obtained by plotting the determined weights against the products of mean body length and mean body width of one male and one

female of each species. Total counts of each species trapped were used to give figure 36. The sexes were taken as equal except in *Procladius choreus*, for which weights of males and females were found and the ratio 1 : 1.48 used.

It can be seen that, if the profundal annual crop is taken as 3.0 gm. per sq. m., this is only 60 per cent. of the March biomass. Figure 36 also shows that the annual crop is higher in the profundal than in the littoral. In fact, however,

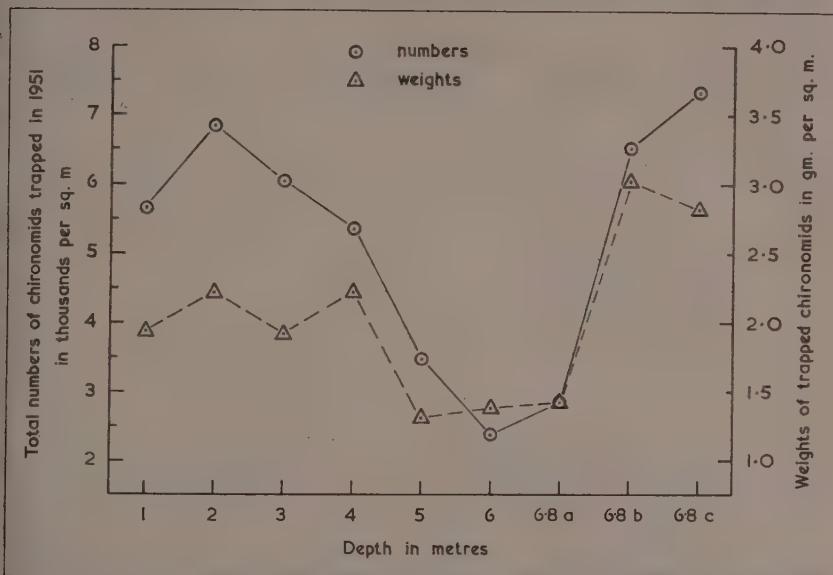


FIG. 36.—Numbers and dry weights of the total annual catch of chironomids at different depths in Kempton Park East Reservoir during 1951.

the opposite certainly holds and the lower catches in the littoral are due to predation by fish. As has been pointed out (p. 214), the low figures for trap 7 (6.8 m. a) are attributed to faulty sampling.

These data, then, give minimal annual crop estimates and establish the increase of weights to numbers with increase in depth. They are at variance with the high rates of turnover deduced by Miller (1941: 57), and with the net production figures of Borutzky (1939a, b) which, for *Chironomus plumosus* and *Tanytus*, were 91 per cent. and 74.5 per cent. respectively of the spring larval biomass. These authors' estimates each involved certain assumptions. The reservoir figure is certainly too low on account of the sampling procedure on which it is based.

It has been pointed out that the genera *Tanytarsus* and *Endochironomus* are mainly phytophagous, that *Chironomus* consists of browsers on detritus and that *Procladius* and *Psilotanytus* are predators. The percentages of herbivores, detritus eaters and carnivores in the standing crop in June and September are given on p. 205. The percentages of these in the total annual emergences from 6.8m. are given for numbers and weights in Table XVIII. It is seen that

the carnivores predominate in the annual crop. This predominance may be real, or it may be the result of selective trapping. In this connection it is noteworthy that it was *Tanytarsus* which formed the most conspicuous swarms on the reservoir banks. This may be interpreted as signifying a much higher density of *Tanytarsus* species than of the Tanypodinae, and hence a selection in trapping; or it may be considered to show merely the weaker capacity of the Tanypodinae to form swarms. The first interpretation seems the more likely.

It would be erroneous to arrange the chironomids in a pyramid of primary and secondary consumers, for it is not known to what extent the one is food for the other. There are two major discernible trophic series in a lake: the

TABLE XVIII.—*The percentage composition of the total annual catches in 1951 in traps 8 and 9 at 6-8 m. in Kempton Park East Reservoir.*

	Numbers.	Weights.
<i>Procladius choreus</i> and <i>P. crassinervis</i>	51	61
<i>Psilotanytus rufovitatus</i>	31	15
<i>Chironomus plumosus</i>	2	17
<i>Endochironomus albipennis</i>	1	2
<i>Tanytarsus holochlorus</i>	11	4
<i>T. lestagei</i>	2	<1
<i>T. lugens</i>	1	<1

well-known nutrient salts, phytoplankton, primary and secondary consumers series; and the other involving the deposition of dead plant and animal material and faeces, the conversion of this to protoplasm by micro-organisms and detritus eaters, and finally the utilisation of the detritus eaters by carnivores. These series are interlinked but the trophic relations between them may be pictured as multidirectional or turbulent rather than unidirectional or streamlined. It is from this complex that the food relationships and hence the mechanism of population control in the various species of chironomids has to be elucidated.

VIII. CONCLUDING REMARKS.

The study of chironomids can be seen, historically, to have followed two main lines which may be termed the limnological and the entomological. One has been concerned with the distribution of different kinds of chironomids in different lakes, with the association of these with lake types, and with numbers and weights of chironomids as aspects of lake productivity. The other has dealt with the biology of particular species, with their feeding habits, respiration, behaviour, voltinism, etc. These two lines converge at one point, the central issue in ecology, *i.e.* the problem of the natural control of populations.

The role of surveys in ecological research, directed towards the ultimate elucidation of this problem, has been depicted by Elton and Miller (1954), whose discussion places many of the points raised in this work in a general ecological context.

Since the value of a survey depends very largely on the reliability of its quantitative findings, the greatest limitation of the present work is the absence of knowledge of exactly what occurs when an emerging population is sampled

by emergence traps. One obvious question which this raises is: how different would the results have been if the traps had been emptied more often than twice weekly? This could easily be investigated, and recently Borutzky (1955) has devised a trap, the jar of which contains preserving liquid, so that successive catches accumulate and the optimum sampling period need not be established.

A degree of uncertainty, which must be regarded as unsatisfactory, is attached to the interpretations of several of the findings. For example, the explanation of the fluctuations of larval numbers in winter and spring requires substantiation; the length of the life-cycles of species in relation to temperature requires more critical treatment than has been given here; anomalous emergences such as those of *Tanytarsus holochlorus* have yet to be explained; the voltinism of *T. lugens* is not certain; the reversal of predominance in numbers from larval *Tanytarsus* to trapped Tanypodinae is open to more than one interpretation; and the role of water movements in the distribution of the fauna is very ill-defined.

It should be noted that the histograms of emergences have all been interpreted as involving successive, not alternating, generations. Whilst it seems most unlikely that the latter develop to any significant extent in small shallow bodies of water, their possible existence should not be overlooked.

A survey is thus as much concerned with defining problems as with solving them. It can nevertheless produce results of general significance. One of these, and perhaps the most unexpected, is the fluctuations in larval numbers in winter and spring. Another is provided by the phenological data.

It is clear that the phenology of chironomids is not determined simply by temperature, but is an adjustment to a total environment. The anaerobic conditions of the mud which may develop in summer in eutrophic lakes must have a rigorous selective action on the fauna and it is in a response to them that the explanation of phenology is to be sought. Brundin (1951) has pointed out that the profundal chironomids emerge and oviposit in direct relation to the spring and autumn circulations of the lake, when oxygen stratification is eliminated. Thus the first instar larva finds itself in an oxygenated habitat. There seems no doubt that such is the adaptive significance of phenology, but with multi-voltine species the adverse season cannot be avoided. These, however, may live below both deep and shallow waters and the littoral population can replace losses encountered in the profundal.

One unexpected feature brought out by the survey is the degree of stability of the fauna in successive generations. It is remarkable that the density of the overwintering generation of most species is of the same order of magnitude as the summer ones. Exceptions to this are *T. lugens* and *T. lestagei* in the profundal and certain species such as *Cricotopus sylvestris* and *C. dizonias* in the littoral. Littoral fluctuations can be attributed to variation in the density of benthic algae, the changes in the profundal population to the selective effect of the adverse summer conditions. Nothing is known about annual fluctuations in numbers and quality except that *Chaoborus* was scarce in 1954. Lundbeck (1926) noted marked quantitative differences in the annual production of bottom fauna in different years in the Grosser Plöner See, and Lindeman (1942a) found qualitative annual fluctuations in Cedar Bog Lake.

The extreme suitability of reservoirs for chironomid studies needs no emphasis. This lies not only in the uniformity of the depth zones, in the high

faunal densities (in eutrophic reservoirs), in the ease with which reservoirs allow rates of replacement of water and changes in water chemistry and algal content to be measured, but also in the fact that reservoirs of different depth, supplied with water from the same source, bring out the real significance of depth in relation to the composition of chironomid communities.

Two points concerning methods may be mentioned. Core sampling would be made much more practicable if the larvae could be quickly and efficiently extracted from the mud and counted. Possibly only treatment of fresh cores offers a prospect of this.

A method which was not used in the survey but which would have given additional information is that of sampling the pupal skins washed ashore (Thienemann, 1954 : 274). Analysis of these would have established the ratio of *Tanytarsus* to Tanypodinae pupae, and perhaps have determined whether or not the traps were selective. It might even be possible, in a reservoir, to relate numbers of skins washed ashore in a given time to numbers of trapped insects, and so to establish the efficiency of the traps.

Many aspects of the biology of the midges could be mentioned which the survey did not touch. Conspicuous among these are the detailed larval taxonomy, the reproductive biology of the species, the exact feeding habits of the larvae, the nature of the community at 0-1 m. which must have features peculiar to itself, the specific causes of larval mortality and the significance of dispersal of the adults from one reservoir to another. The analysis of these matters will require the elaboration of new techniques.

IX. SUMMARY.

1. A survey has been made of the Chironomidae of Kempton Park East Reservoir (area 16.1 hectares, maximum depth 7 m.) in Middlesex to establish the qualitative and quantitative distribution of the species at each metre depth zone, the sequence of their emergences throughout the year, and their voltinism; and to estimate the standing crop of larvae and the total annual crop of emerging adults from different depths in the reservoir.

2. The bulk of the data was obtained by trapping emerging chironomids in 27 submerged traps laid out in three transects from shallow to deep water and emptied twice weekly. The technique was found to have several sources of error and estimates of its efficiency varied from 1 per cent. to 79 per cent. for different species and groups of species.

On the basis of the trapping results pupal, or larval and pupal, mortality at 1 m. was three times that at 6-8 m.

3. The emergence data for most of the trapped species are given as histograms which show, ideally, the depths at which a species occurs, its optimum depth, the number of generations it has in a year at different depths, the dates of emergence, the skewness and kurtosis of the distribution and the effect of increase in depth on time of emergence.

4. The fauna was found to consist of 38 trapped species and 20 others found only in swarms. The distribution of the commoner species, based on the total annual emergences at each depth, is shown graphically in figure 7.

5. The distributions of the species are discussed with reference to their feeding habits and respiratory requirements.

A brief account is given of insects other than chironomids found in the reservoir. The most abundant of these was *Chaoborus flavicans* Meig.

6. For the quantitative investigation of the larvae in the profundal a Jenkin surface mud sampler was used. A benzene and water treatment was adopted for separating the larvae from mud. In the profundal 95 per cent. of the larvae were found to lie in the uppermost 5 cm. of mud. The mean standing crop of larvae at 6.8 m. in March, 1952 was 34,000 per sq. m.; in the littoral at 1 m. it was 46,000 per sq. m.

7. In late winter and in spring the larval population at 6.8 m. showed marked fluctuations in numbers. It is suggested that these are caused by wind-induced water movements disturbing the mud and larvae, so that the larvae enter the water mass.

8. The larval population at 6.8 m. in June and September consisted of about 73 per cent. *Tanytarsus* and 22 per cent. Tanypodinae. The emergences, however, of the Tanypodinae were nearly five times as great as those of all other species taken together. The mortality of *Tanytarsus* larvae is, therefore, high, or the traps act selectively in favour of the Tanypodinae. The second interpretation is considered to be more probable.

9. Certain anomalous emergences could not be explained; for example the apparent occurrence, as recorded by trapping, of emergences of *Procladius choreus* and *Tanytarsus holochlorus* from the littoral in one year but not in another, and of *T. holochlorus* from the profundal in one year but not in another.

10. The dry weight of the larvae at 6.8 m. in March, 1952 was 5.25 gm./sq. m. (46 lb. per acre). The dry weight of the total annual emergences in 1951 at 6.8 was 3.0 gm./sq. m. or 60 per cent. of the late winter standing crop.

11. Trapping was also carried out on Staines South Reservoir (area 99.5 hectares, max. depth 9 m.). Here 26 species were found. Staines South Reservoir has a *Procladius choreus*, *Tanytarsus lugens*, *Chironomus plumosus*, *Chironomus anthracinus* profundal community. The same community was found in Queen Mary Reservoir (area 292 hectares, max. depth 10.5 m.) to which observations were extended.

The differences between the profundal community of these reservoirs and that of Kempton Park East Reservoir are attributed to the greater depth which, by imposing a greater stability on stratification, brings about a high oxygen concentration deficit in summer.

12. Aspects of productivity of chironomids are discussed. The relationship between chironomid type and lake type is reviewed and shown to lie through the benthic oxygen as a limiting factor to chironomid distribution.

13. Limitations of the survey are discussed and lines of future work indicated.

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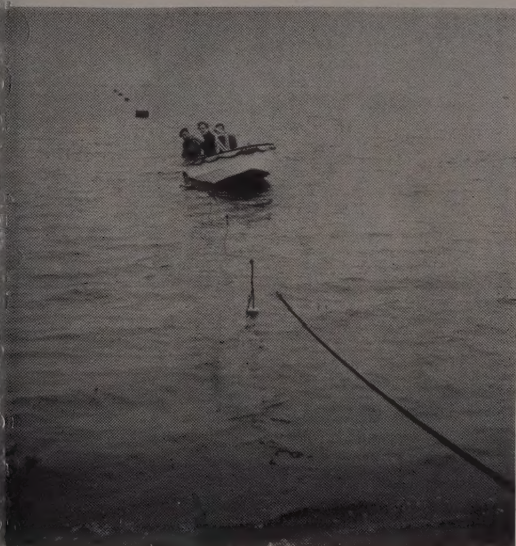
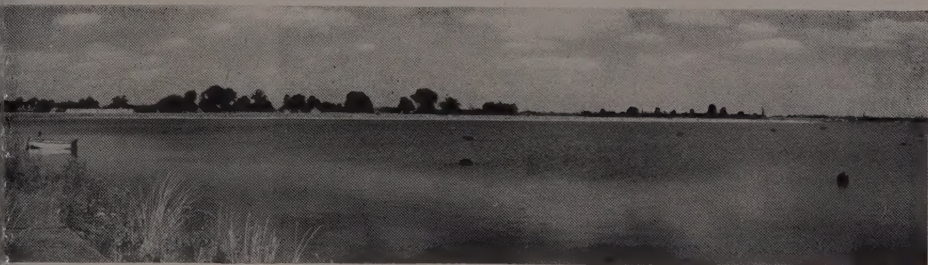
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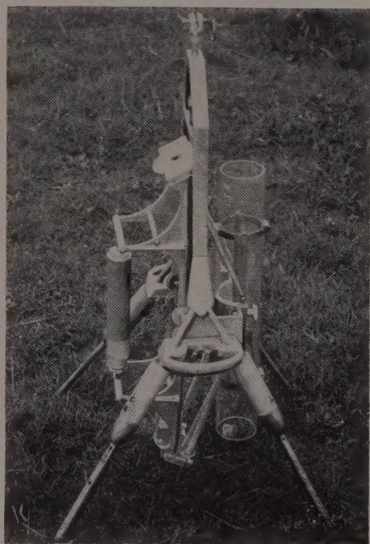
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(b)



(c)

(a) Panoramic view of Kempton Park East Reservoir (Photo: J. W. Siddorn).

(b) A line at Kempton Park East Reservoir lifted to show the jar of the trap at 1 m. (Photo: B. M. Gorringe).

(c) The Jenkin surface mud sampler (Photo: J. W. Siddorn).

The ecology of Chironomidae in storage reservoirs.

